Impact of the invasive ant *Linepithema humile* on native ant assemblages on the western slopes of Table Mountain and implications for ant-butterfly associations

André Krahner

Supervisor: Dr. Mike Picker

Percy FitzPatrick Institute of African Ornithology
Zoology Department
University of Cape Town
Rondebosch,
South Africa 7701

February 2011

Submitted in partial fulfillment of the requirements for the degree of

Master of Science in Conservation Biology

DECLARATION

I hereby:

(a) grant the University free license to reproduce this dissertation in whole or in part, for the purpose of research;

(b) declare that:

(i) the above dissertation is my own unaided work, both in conception and execution, and that apart from the normal guidance of my supervisor, I have received no assistance apart from that stated in the acknowledgements;

(ii) neither the substance nor any part of the thesis has been submitted in the past, or is being, or is to be submitted for a degree at this University or any other University.

(iii) I am now presenting the dissertation for examination for the project component of the Degree of MSc by coursework.

(iv) No part of this dissertation has been plagiarized

Signed: Date:

οὐδὲν γὰρ οὕτω μικρὸν ἡ φύσις ἔχει
μειζόνων καὶ καλλιόνων κάτοπτρον,
ἀλλ᾽ ὥσπερ ἐν σταγόνι καθαρᾷ
πάσης ἔνεστιν ἀρετῆς ἔμφασις,
ἔνθ᾽ ἔνι μὲν φιλότης τὸ κοινωνικόν,
ἔνι δ᾽ ἀνδρείας εἰκὼν τὸ φιλόπονον.

Πλούταρχος, Ἠθικά

Nature has, in fact, nowhere else so small a mirror of greater and nobler enterprises. Just as you may see greater things reflected in a drop of clear water, so among ants there exists the delineation of every virtue. Love and affection are found, namely their social life.

Plutarch, Ethika

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

First, I would like to thank my supervisor, Dr. Picker, University of Cape Town, for the many useful suggestions, his all-time willingness to assist, and also for providing material equipment. Further, I thank Terry Trinder-Smith, University of Cape Town, for introducing me to the Bolus Herbarium and for his hospitality. I am indebted to South African National Parks, in particular Ruth-Mary Fisher, for issuing the research permit necessary for fieldwork in Table Mountain National Park. I also thank Chad Cheney and Philip Prins of South African National Parks, who gave access to the spatial data of the Fire Management Database as of 2010. I am also indebted to the City of Cape Town, in particular to Amalia Stipinovich, who gave access to the spatial vegetation data for the Cape Peninsula and to spatial data of the Biodiversity Network of the City of Cape Town. Finally, I would like to thank Margie Cochrane, Iziko South African Museum Cape Town, for providing working facilities and access to the Hymenoptera specimen collection.

Factors that promote invasions of *Linepithema humile*

Based on the degree of invasiveness and ecosystem impact, the Argentine Ant, *Li. humile* (Mayr), is one of, if not the most important invasive ant worldwide (Holway et al. 2002a). In South Africa *Li. humile* is one of comparatively few naturalized invasive animal species (Deacon 1986). The ant was first reported in this country from the Cape Peninsula in 1908 (Skaife 1962), where it is thought to have been introduced unintentionally in cargo, and subsequently spread inland and east along the coast (Skaife 1961). Likewise, worldwide introductions of *Li. humile* have followed trading routes (Majer 1994). Today, there seems to be one giant supercolony plus the occasional presence of a few smaller supercolonies on each continent except Antarctica (Suarez et al. 2001; Holway et al. 2002a; van Wilgenburg et al. 2010). Europe is inhabited by only two supercolonies, the larger of which ranges at least over 6000km (Giraud et al. 2002), and Australia appears to be home for one vast supercolony (Suhr et al. 2009). The effective occupation of four continents by a single supercolony has been suggested, while the supercolony from South Africa seems to be different from this unit (van Wilgenburg et al. 2010).

Linepithema humile invasions seem to be strongly affected by abiotic factors such as water availability and temperature. Compared to xeric-adapted native ants from coastal southern California, *Li. humile* has a higher rate of spiracular and cuticular water loss (Schilman et al. 2005). The ant invasion expands along perennial, but retreats along seasonally intermittent watercourses (Holway 1998), and abundance of *Li. humile* decreases with increasing distance from riparian corridors (Holway 2005). Although average precipitation is a poor predictor of *Li. humile* abundance at the landscape scale (Menke et al. 2007), annual variation in abundance of *Li. humile* is correlated with winter rainfall at the local scale (DiGirolamo & Fox 2006). High annual precipitation increases the rate of invasion, and irrigation enables (Menke et al. 2007) or facilitates the invasion of *Li. humile* (Menke & Holway 2006).

Another factor determining habitat invasibility for *Li. humile* is temperature. Compared to native ants in California (Holway et al. 2002b) and Australia (Walters & Mackay 2004), *Li. humile* is less tolerant of high temperatures. The ability to spread from mesic into dry habitats appears to be limited by hot and dry environments, as dominant native ants are better adapted to low humidity levels than *Li. humile* (Walters & Mackay 2003a) and competitive

superiority of *Li. humile* against native species is depressed under high temperatures (Thomas & Holway 2005). On the other hand, low temperatures probably limit the spread of *Li. humile* into natural habitat with closed canopies in New Zealand (Ward & Harris 2005) and minimum winter temperature is positively correlated with abundance of *Li. humile* (Menke et al. 2007). Finally, correlative models, which aim at predicting invasible areas based on climatic modelling, project an expanding range of *Li. humile* in higher latitudes in the course of global climate change (Roura-Pascual et al. 2004). However, insights from these models are limited by incorporation of only a subset of the factors determining the range of a species (Roura-Pascual & Suarez 2008).

Social insects use cuticular hydrocarbon (CHC) profiles, also referred to as colony odor, to discriminate between nestmates and non-nestmates (d'Ettorre & Lenoir 2010), and nestmate recognition in *Li. humile* has been investigated by means of aggression bioassays. Presence of at least two cuticular-hydrocarbon classes is necessary to trigger aggressive behavior in *Li. humile* (Greene & Gordon 2007). CHC profile and nestmate recognition in *Li. humile* can be modified by food composition, resulting in aggressive behavior among former nestmates (Liang & Silverman 2000) or reduction of moderate aggressiveness between colonies (Buczkowski et al. 2005). In addition, social context seems to affect nestmate recognition (Vasquez & Silverman 2008). However, information from aggression bioassays in the laboratory might be of limited value for the investigation of interaction between colonies in the field (Roulston et al. 2003), and effects of CHC alteration on colony structures in the wild remain unknown (Steiner et al. 2010).

Introduced populations of *Li. humile* generally show a low diversity in recognition cues. Although areas subjected to multiple recent introductions are inhabited by several genetically distinct populations (Hirata et al. 2008), areas with a long history of multiple introductions are dominated by one genetically identical population (Giraud et al. 2002).

A population bottleneck in the course of introduction has been suggested as a potential reason for low genetic diversity and subsequent low levels of intraspecific aggression in introduced *Li. humile* populations (Tsutsui et al. 2000). On the other hand, selection against genetic diversity has been suggested as playing a key role in the formation of unicoloniality in Europe, where a history of successive introductions would make a serious bottleneck unlikely (Giraud et al. 2002). In contrast to earlier findings (Tsutsui & Case 2001), however, unicoloniality and the existence of supercolonies are also observed in the native range of *Li.*

humile, making the size of supercolonies the only apparent difference between introduced and native populations (Pedersen et al. 2006; Vogel et al. 2009).

Unicoloniality allows for nest fusion and enables workers and queens of *Li. humile* to mix freely among nests (LeBrun 2010). By contracting the colony network to limited suitable sites in times of abiotic stress, and expanding the network under less stressful conditions, *Li. humile* is able to make use of space in a highly opportunistic manner (Heller & Gordon 2006). This ability of *Li. humile* probably evolved as an adaptation to seasonal inundation of the Paraná-River floodplain, where native populations track resources on seasonally receding and appearing dry ground (LeBrun 2010). Unicoloniality enables *Li. humile* to build up supercolonies covering vast areas in introduced ranges, with individual nests being connected over distances of up to 50m (Heller et al. 2008a). Furthermore, in the introduced range seasonal patterns of expansion and contraction of colony networks in response to abiotic conditions (Heller et al. 2006) result in corresponding inter-annual expansion and contraction of the invasion front (Sanders et al. 2001; Heller et al. 2006).

The dominance of colonies is generally increased by polydomy (Roura-Pascual & Suarez 2008). For example, polygynous-polydomous populations of *Formica* species in general rank higher in the dominance hierarchy of the ant community than monogynous-monodomous populations of the same species (Steiner et al. 2010). Dominance of *Li. humile* can be observed at baits, which it generally monopolizes (Walters & Mackay 2003b; Rowles & O'Dowd 2007; Buczkowski & Bennett 2008a, b; Carpintero & Reyes-Lopez 2008). However, abiotic factors can prevent resource monopolization (Thomas & Holway 2005), and it has been suggested that *Li. humile* cannot achieve ecological dominance in the absence of honeydew resources (Addison & Samways 2000). Also, resource monopolization by *Li. humile* seems to be dependent on the lack of intraspecific aggression (Holway & Suarez 2004) and large colony size (Walters & Mackay 2005).

While in riparian corridors the rate of invasion by *Li. humile* is independent of native ant richness, underlining the importance of abiotic conditions for the rate of spread (Holway 1998), in irrigated areas native ants seem to slow down the invasion of *Li. humile* (Menke et al. 2007). Likewise, competition of dominant Dolichoderinae (*Iridomyrmex* spp.) has been suggested as one reason why invasive ants do not spread easily into natural habitat in Australia (Majer 1994; Andersen 1997), while underrepresentation of dominant Dolichoderinae seems to be a factor for the susceptibility of North American ant communities

to *Li. humile* invasion (Andersen 1997). Factors causing losses of native species might contribute to invasion of alien invasive species in urban areas (Holway & Suarez 2006).

Impact of *Li. humile* on native ant and other arthropod communities

Li. humile displaces native ant species through interference competition (Human & Gordon 1996; Holway 1999), although predation might also play a role (Zee & Holway 2006). By displacing native ant species, *Li. humile* reduces species richness in invaded areas (Holway et al. 2002a; Lach & Hooper-Bùi 2010). In the Fynbos, three out of five native ant species were displaced in the course of *Li. humile* invasion into study areas (Bond & Slingsby 1984).

By displacing particular native ant species, in particular larger-bodied ants, composition of ant communities is altered at invaded sites, probably affecting ecosystem processes (DiGirolamo & Fox 2006; Walters 2006; Glenn & Holway 2008). *Linepithema humile* invasion apparently results in the alteration of co-occurrence pattern within native communities (Sanders et al. 2003). While segregation among ant species is the predominant co-occurrence pattern in native ant communities, co-occurrence structure of invaded communities is shifted towards aggregation. Not only does *Li. humile* displace epigaeic (ground foraging) ants, but displacement of arboreal species has also been reported (Carpintero et al. 2005). Lastly, the negative impact of *Li. humile* on species richness appears to be most severe in the early phases of invasion, as the number of species subsequently increases in time at invaded sites, although not reaching levels corresponding to non-invaded sites (Heller et al. 2008b).

In addition to impacts on species richness, *Li. humile* invasions reduce the abundance of native ant species at invaded sites. At invaded sites in south-eastern Australia native epigaeic ants are either absent or markedly reduced in individual number (Rowles & O'Dowd 2009a), while in southern California abundance of native ants and *Li. humile* are negatively correlated (Holway 2005). Also, at invaded sites in the Fynbos vegetation, *Li. humile* individuals account for the largest fraction of ants sampled in pitfall traps by far (Bond & Slingsby 1984).

Behavioral changes of native ants in response to presence of *Li. humile* include decreased foraging (Holway & Suarez 2004; Zee & Holway 2006) or altered foraging strategy (Carpintero et al. 2007), changed colony structure (Holway & Suarez 2004; Zee & Holway

2006), and lowered rate of reproduction (Holway & Suarez 2004). Ecologically similar native ants are particularly affected with regard to behavioral changes, while alterations in subordinate species and those with a different temporal activity are less pronounced (Carpintero et al. 2007).

Studies about effects of *Li. humile* invasion on non-formicid arthropod abundance yield mixed results, ranging from insignificant effects (Walters 2006; Rowles & O'Dowd 2009a) to increased numbers of crustaceans (Walters & Mackay 2003b), Psocoptera (Rowles & O'Dowd 2009a), and myrmecophagous Salticidae (Touyama et al. 2008), as well as depressed abundances of Carabidae (Liebherr & Krushelnycky 2007) at invaded sites. Most importantly, *Li. humile* invasion results in lower individual numbers of lepidopteran larvae (Rowles & O'Dowd 2009a).

Impact of *Li. humile* on interspecific associations

In addition to direct impacts of *Li. humile* on other species, a substantial record exists of its impact on interspecific associations. Although invasion of *Li. humile* does not necessarily translate into altered reproductive success of myrmecochorous plants (Oliveras et al. 2005), by displacing native ant species *Li. humile* invasion can impact on regeneration of myrmecochorous plant species (Rowles & O'Dowd 2009b). In the Fynbos vegetation, seedling recruitment and abundance in *Mimetes cucullatus* are strongly affected by *Li. humile* (Bond & Slingsby 1984). Native seed-dispersing ants such as *Anoplolepis custodiens*, *Meranoplus peringueyi* and *Pheidole capensis* quickly recover seed exposed on the soil and carry most to their nests where they devour the nutritive elaiosome, while *Li. humile* does not bury seeds, moves them over much shorter distances and consumes the elaiosome on the surface. Seed remains more exposed in areas invaded by *Li. humile*, resulting in greater seed predation through rodents and less recruitment of myrmecochorous plants (Bond & Slingsby 1984; Bond & Breytenbach 1985). Thus, through suppression of native ant species diversity, *Li. humile* indirectly alters plant-community composition in the Fynbos (Christian 2001).

Attracted to various plants by floral nectar, *Li. humile* displaces pollinators from a wide taxonomic range, including Diptera (Blancafort & Gomez 2005), Formicidae (Blancafort & Gomez 2006), Apidae (Lach 2008a, b), Coleoptera (Lach 2007), and other taxa (Lach 2008a). Furthermore, *Li. humile* is known to alter the composition of the parasitoid community and to decrease overall parasitism associated with galls on *Quercus lobata* (Inouye & Agrawal

2004). In the Fynbos, formation of a new mutualism between native Membracidae and *Li. humile* enables the ant to discover inflorescences more quickly, thereby increasing the rate of displacement of other native arthropods from the plant (Lach 2007). In southern Europe, a decrease in pollinators of *Euphorbia characias* under *Li. humile* invasion resulted in reduced fruit and seed set (Blancafort & Gomez 2005).

Associations between lycaenid butterflies and ants

A well-known relationship exists between most genera of lycaenid butterflies and ants. Many species in the family Lycaenidae are associated with a particular species of ant (Appendix 1). This association is obligatory for many Lycaenidae in order to complete the life-cycle (Henning 1983a; Heath & Claassens 2003). It varies from one species to another and ranges from mutualism (Fiedler & Saam 1995) and commensalism (Pierce & Young 1986) to parasitism (Thomas & Wardlaw 1992; Heath & Claassens 2000). For example, in mutualistic associations butterfly larvae that are ant-attended while feeding may offer nectar in exchange for indirect defense (Agrawal & Fordyce 2000), while parasitic butterfly larvae usually spend their later ontogenetic stages in the ant nest, being fed by ants through trophollaxis or feeding on formicid pupae or larvae (Clark & Dickson 1971; Henning 1983a; Claassens 2000). These lifestyle variations are generally reflected by associated anatomical adaptations. These appear as a dorsal nectary organ (DNO) producing a substance comparable to the honey-dew excreted by aphids (Clark & Dickson 1956; Malicky 1969), in form of pore cupola organs (PCO), small epidermal glands probably producing volatile substances attracting or pacifying ants (Malicky 1969; Henning 1983b), and as tentacle organs (TO), which emit volatile substances attracting and alerting host ants (Henning 1983b; Pierce et al. 2002). Moreover, widespread larval and pupal sound production in the Lycaenidae mediates ant-butterfly associations (Claassens 1991; DeVries 1991; Travassos & Pierce 2000; Pierce et al. 2002).

In Australia, 39 out of 56 lycaenid butterflies that are obligatorily associated with ants have distributions overlapping with the invasive ant species *Li. humile*, *P. megacephala* or *Ano. gracilipes*, and one is now known to have developed an association with *Li. humile* (Lach & Thomas 2008). For the Cape Peninsula, there are reports on associations between three facultatively myrmecophilous lycaenids, which are mutualistically associated with native ants, as well as *Li. humile*: *Anthene definita* (Claassens & Dickson 1980), *Lampides boeticus* (Clark & Dickson 1971), and *Tarucus thespis* (Dickson 1944) (Appendix 1). *Li. humile* is

attracted by secretions that are rich in carbohydrates (Holway et al. 2002a), and laboratory studies indicate, that inducible nectar excretion and indirect defense through attendant ants stabilize ant-lycaenid mutualisms (Agrawal & Fordyce 2000). However, it is unknown if benefits of mutualistic ant-butterfly associations are shared to the same degree if the native ant is replaced by *Li. humile* (Lach & Thomas 2008).

Presence of the right host ant, just like presence of the correct host plant, is often a fundamental factor in determining habitat suitability for lycaenid butterflies (Wynhoff et al. 2008). Butterfly density in ant-associated Lycaenidae at the landscape-scale is correlated with presence and abundance of the host ant, as it depends on pupal and larval association with host ants at the local scale (Jordano et al. 1992). Further, host ants are used as oviposition cues by female Lycaenidae (Atsatt 1981; Henning 1983a; Wagner & Kurina 1997), including the South African genera *Aloeides* and *Chrysoritis* (Cottrell 1984), as well as *Thestor* (Williams & Joannou 1996). Laboratory experiments with European Lycaenidae indicate low specificity of butterfly interactions with regard to host ant (Malicky 1969), but relationships involving only a single host ant species are widely distributed among lycaenid subfamilies and include the genera *Lepidochrysops* and *Thestor* (Cottrell 1984), which are present on the Cape Peninsula (Appendix 1).

There is a general lack of research on the ecological impact of invasive ants on myrmecophilic arthropods (Holway et al. 2002a). *Li. humile* has a demonstrated ability to depress numbers of ant genera and species which are known hosts of Cape lycaenid butterflies. Assessing the impact of *Li. humile* on the Lycaenidae will allow for evaluating the efficiency of protected areas in conserving lycaenid butterflies in the longer term. As lycaenid species are important contributors to faunal endemism of the Cape Peninsula (Claassens & Dickson 1980; Henning & Henning 1989), their conservation deserves highest attention.

As many of the indirect effects of *Li. humile* on ecosystem processes are mediated through compositional changes in local ant assemblages, an assessment of the impact of *Li. humile* on native ant species is of fundamental importance for conservation of natural habitats. Given the high turnover rate in ant species composition on the one hand (Boonzaaier et al. 2007), the high complexity of abiotic factors influencing invasion success of *Li. humile* on the other, the impact of this invasive ant has to be assessed at the local level. Doing so will result in a better evaluation of conservational value of protected areas on the Cape Peninsula.

Impact of the invasive ant *Linepithema humile* on native ant assemblages on the western slopes of Table Mountain and implications for ant-butterfly associations

---

ABSTRACT

The Argentine Ant, *Linepithema humile* (Hymenoptera: Formicidae), is one of the world's most successful invasive species and invades undisturbed Fynbos habitats in South Africa, displacing native arthropod species and affecting interspecific associations. In order to assess the impact of *Li. humile* on native ant assemblages and associations between ants and myrmecophilous butterflies (Lepidoptera: Lycaenidae) on the western slopes of Table Mountain (Cape Town, South Africa), adult butterfly density was scored and distribution of food plants were assessed at two sites. Further, ant assemblage composition was investigated using unbaited pitfall traps at 10 sites. Six myrmecophilous lycaenid species were observed, with *Aloeides thyra thyra* and *Al. pierus* being the most common. However, as adult butterflies aggregated far from the larval food plant (*Aspalathus* spp.), imagines appear to have dispersed from their site of emergence, rendering the abundance of imagines uninformative for a local-scale assessment of associations between ants and lycaenid larvae. Only two of 10 transects were considered invaded by *Li. humile*. No significant differences between the native ant communities of Invaded and Non-Invaded transects were observed regarding abundance, occurrence and species richness. Abundance of Generalized Myrmicinae, and abundance as well as occurrence of the lycaenid-associated ant *Lepisiota capensis*, were markedly lower in Invaded than in Non-Invaded sites, while Subordinate Camponotini were more abundant and occurred in more traps in Invaded transects compared to Non-Invaded. Bray-Curtis similarity among Invaded and Non-Invaded ant assemblages was low, and only one Non-Invaded ant assemblage showed a species co-occurrence pattern significantly different from random co-occurrence. *Li. humile* appears to have a weak impact on native ant communities, including host ants of lycaenid butterflies, compared to other factors within the study area. Thus it appears not to pose an immediate threat to lycaenid butterflies in the study area. As this snapshot study is incapable of assessing seasonal and inter-annual changes in the invasion front of *Li. humile*, present results are likely to underestimate the impact of *Li. humile* on native ants.

INTRODUCTION

Apart from direct competitive and consumptive impacts on biota, many invading species have the potential to disrupt species interactions, and thus indirectly impact on ecosystem processes, often with cascade effects. Originating from South America, the Argentine Ant, *Linepithema humile*, is one of the most successful invasive species in the world, probably due to its supercoloniality (formation of networks of mutually tolerant individuals in colonies with several queens) (Tsutsui et al. 2000) and the resulting competitive advantages against native ants (Holway 1999; Holway & Suarez 2004) outside its native range. Invading Mediterranean and temperate climatic regions worldwide, *Li. humile* displaces native epigaeic (above-ground foraging) ant species (Skaife 1962; Donnelly & Giliomee 1985; Ward 1987; De Kock & Giliomee 1989; Carpintero et al. 2004; Rowles & O'Dowd 2009a), depresses native arthropod diversity (Human & Gordon 1997), alters community structure in native ant assemblages (Sanders et al. 2003), and disrupts mutualisms in the South African Fynbos (Bond & Slingsby 1984; Christian 2001; Lach 2007). *Li. humile* has been present on the Cape Peninsula since at least 1908 (Skaife 1962).

With 67 species permanently inhabiting the Cape Peninsula (Claassens 2000), butterflies are one of the key contributors to insect diversity in the region. More than half of the butterflies belong to the family Lycaenidae (Claassens 2000) (Appendix 1), whose conservation status gives rise to concern. Three out of 35 species are endemic to the Cape Peninsula, two to the Western Cape (Henning & Henning 1989; Claassens 2000), and three species are protected by law (Henning & Henning 1989). Four species have been classified as Rare, Vulnerable or Endangered (Henning & Henning 1989), two of which are listed as Vulnerable in the IUCN Red List (IUCN 2010). The larvae of at least 21 out of 35 lycaenid species are myrmecophilous (Clark & Dickson 1971; Claassens & Dickson 1974, 1980; Claassens 2000; Heath & Claassens 2003), i.e. they are associated with ant species, and this is true for five out of six threatened species.

For many phytophagous, phyto-predacious, and predacious larvae as well as secretion feeders within the Lycaenidae, an association with a particular ant species is obligatory in order to complete the life-cycle (Henning 1983a; Heath & Claassens 2003). Many phytophagous larvae need the attendance of native ants on the foodplant, while predacious larvae often undergo part of their development within the nest of their host ant. Myrmecophilous larvae also show anatomical features in concordance with their life style. These appear, for example,

METHODS

Study Area

The main study was undertaken on the western slopes of Table Mountain, below the Twelve Apostles and above Camps Bay (City of Cape Town, Western Cape Province, South Africa; S33°57'26'' E18°23'28'') (Figure 1). The study area covers an altitudinal range of 210-310m above sea level. Being a part of Table Mountain National Park the study area is under proclaimed protection, but abuts on the urban fringe of the suburb of Camps Bay. The fynbos vegetation is of the North Peninsula Granite type, a fairly dense shrubland, 1-2m in height (Holmes et al. 2008), and belongs to the Cape Floral Kingdom (Trinder-Smith 2006). The plant community is described as Mesic Mesotrophic Proteoid Fynbos (Mucina et al. 2005). Based on recent fire history the study area has an average fire return rate of less than 7.5 years (Forsyth & van Wilgen 2008), and the study area is covered with veld that remained unburnt for the last 4-45 years (South African National Parks 2010) (Figure 1A).

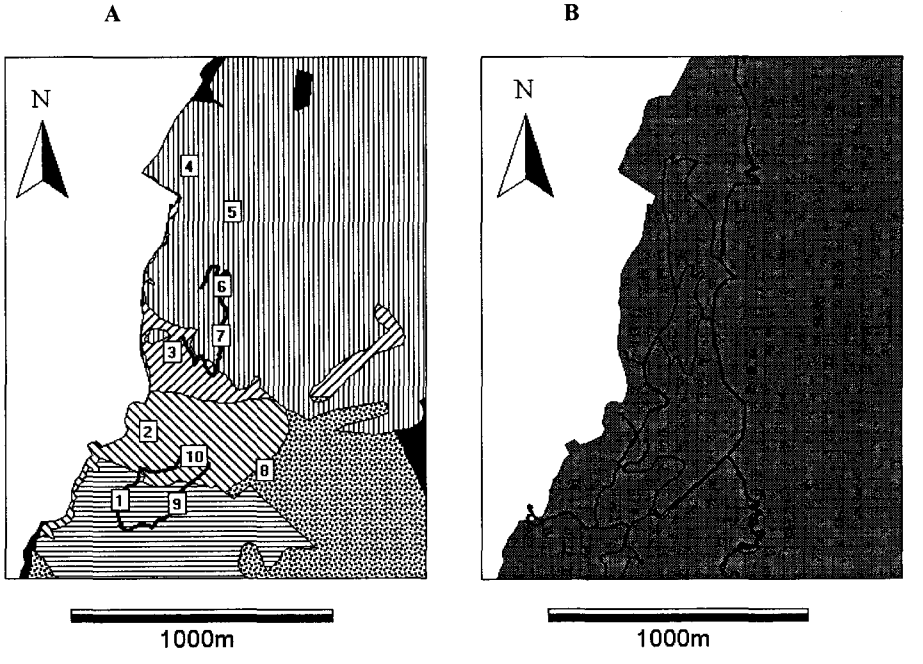

Figure 1. A) Veld age (years since last fire) in the study area above Camps Bay (modified from South African National Parks 2010). Transects 1-10 are represented by numbers 1-10. Bold lines show the two transects for butterfly assessment.
urban area | 4-6 years | 7-9 years | 22-24years | 37-39 years | 43-45 years | other veld age
B) Footpaths within the study area above Camps Bay (modified from Stipinovich & Holmes 2009).
urban area | Table Mountain National Park

A pilot study also included the northwestern slopes of the Lion's Head (S33°55'48'' E18°23'32''). The vegetation in this area is North Peninsula Granite Fynbos and Shale Renosterveld (Holmes et al. 2008), and is covered by vegetation aged 4-6 years (South African National Parks 2010). The climate of the Cape Peninsula is Mediterranean, with most rainfall occurring in winter.

Data Collection

Myrmecophilous butterfly species within the family Lycaenidae were recorded from the footpath along two transects (Figure 1A) on four field trips on warm (above 20°C) and sunny days between 13 September and 2 November 2010, in the morning and early afternoon. Only adults were scored. Butterfly identification was based on color patterns on the ventral hind-wing surface, using the field guides by Migdoll (1992) and Claassens (2000), and the number of individuals encountered was recorded for each species. All butterflies were marked on the ventral surface of their hind-wings, using a permanent marker, to enable identification of individuals on recapture, thereby avoiding recounting the same individual and obtaining data on dispersal of adult butterflies. In order to avoid behavioral changes in response to the treatment (Kemp & Zalucki 1999), butterflies where chilled on an ice block for 3min before and 2min after the marking procedure. All butterflies were released at the site of their capture. The horizontal distance between recapture site and the site of first capture was calculated using a GPS Garmin Vista HCx GPS receiver (accuracy ±10m).

The distribution of *Aspalathus* spp., the food plants of lycaenid butterflies in the genus *Aloeides*, within the study area was assessed. Plants were identified to genus using the key by Trinder-Smith (2003). Plant specimens were then matched to specimens deposited at the Bolus Herbarium (University of Cape Town) and identified to species using species monographs provided in Adamson & Salter (1950).

For the pilot study on Lion's Head, ants were sampled along one 750m and one 350m transect, using 16 and eight pitfall traps, respectively, the opening being 20mm in diameter. The pitfall traps were set at 50m intervals, baited with sugar solution, and left open for two consecutive days from 14 to 16 October and from 17 to 19 October 2010.

For the main study above Camps Bay, ants were sampled using pitfall traps that were made of transparent plastic, the opening being 60mm in diameter. Sampling occurred in 10

transects (Figure 1A), which were selected to cover the heterogeneity of the study area. Each transect was set up along a 100 m long section of a footpath. Traps were set along two lines parallel to the path on both sides in 5 and 10m distance to the path. Along each of the lines, every 20m a pitfall trap was set. Thus the number of traps totaled 24 per transect. Transects were set up several hundred meters apart from each other, to minimize pseudoreplication. Location of the transect center was determined using GPS.

Traps were closed with a lid immediately after they were set up and remained closed for at least 12 days to avoid a digging-in effect (Greenslade 1973). After this incubation period the lid was removed and the trap filled with 40ml ethylene glycol. On each sampling day four pitfalls of each transect were opened. Pitfalls then remained open for six consecutive days. The sampling period started on 20 November and ended on 01 December 2010. This was repeated at intervals until all traps in all transects had been sampled.

Two environmental factors were investigated for each transect viz. closest distance between transects and the nearest watercourse as well as between transects and the nearest tarred road. These were measured using Google Earth v4.2 (Google Inc. 2007) and GPS location of the transect center. Distances were measured horizontally in meters and rounded to closest decade. Location of watercourses was verified by means of GPS data from field trips.

Ants were washed and stored in 75% ethanol immediately after collection of the pitfall traps. Ants were then separated according to morphospecies, enumerated and, relying to large degree on the worker caste, identified to species level using keys by Hölldobler & Wilson (1990), Bolton (1994) and Taylor (2010). For identification purposes, representatives of morphospecies from each transect were mounted on insect pins. Species identification was verified by comparison with type specimens from the Iziko South African Museum Cape Town. Voucher specimens of the present study will be deposited in the collection of the Iziko Museum.

Data Analyses

Abundance data are often misleading in community studies of social insects such as ants due to their aggregative nature (Longino 2000) and their coloniality. Therefore, in addition to abundance, occurrence was analyzed, which is defined as the number of traps per transect in which a particular species was recorded. Transects with an occurrence of *Li. humile* greater

than 40% of the traps were regarded as Invaded Transects, as this percentage is possibly related to the presence of nests within a transect. Transects for which at most 10% of the traps contained *Li. humile* were regarded as Non-Invaded Transects, as this percentage is possibly related to foraging trails and the absence of nests from a transect.

Species richness was assessed for individual transects. Species accumulation curves were obtained using Primer v6.1.5 (Clarke & Gorley 2006), performing 999 permutations of sample order. To assess sampling efficacy, observed species richness and species richness estimators were compared to each other by means of paired t-tests.

Species estimators were calculated using EstimateS v8.2.0 (Colwell 2006). The Incidence-based Coverage Estimator (ICE) (Lee & Chao 1994) and Chao 2 Richness Estimator (Chao 2) (Chao 1987), both based on presence-absence data, were recommended by Chadzon et al. (1998). Although behaving similarly, Chao 2 is more sensitive to spatial patchiness. Exponential Shannon Diversity Index (exp(H')) and Simpson-Yule Index (D) in its inverse form were calculated using EstimateS (Colwell 2006). These two measures and the observed species richness (S_{obs}) are part of the same family of diversity indices and cover a continuum from high sensitivity to rare species (S_{obs}) over equal sensitivity to rare and abundant species (exp(H')) to high sensitivity to abundant species (D) (Jost 2007).

Based on the whole ant species set excluding *Li. humile*, Invaded and Non-Invaded Transects were compared by the observed species richness, species richness estimators, biodiversity indices, abundance and occurrence by means of unpaired t-test or, if this was impossible, Mann-Whitney test.

Further comparisons were made based on functional groups: Generalized Myrmicinae (*Pheidole* spp., *Monomorium* spp.), Opportunists (*Lepisiota* spp., *Technomyrmex* spp., *Tetramorium* spp.), and Subordinate Camponotini (*Camponotus* spp.) (Andersen 2010). Not all *Monomorium* species can be regarded as Generalized Myrmicinae (Andersen 2010) and the status of species found in this study was unknown. Therefore, analyses for Generalized Myrmicinae were performed 1) including all *Monomorium* species and 2) excluding them. Based on functional group, observed species richness, abundance and occurrence were compared between Invaded and Non-Invaded Transects by means of unpaired t-test or, if this was imposible, Mann-Whitney test.

Abundance and occurrence of *Lepis. capensis* and *P. capensis*, both important Lycaenidae-associated ants (Claassens & Dickson 1980; Claassens 2000), was compared between Invaded and Non-Invaded Transects by means of unpaired t-test in GraphPad Prism v5.03 (GraphPad Software 2010).

For multivariate analyses of species composition of the transects, occurrence data for the various ant species, with transects as sites, were analyzed with Primer (Clarke & Gorley 2006), using Bray-Curtis Similarity index (S^{BC}). The resemblance analysis was undertaken by means of Multi-Dimensional Scaling (MDS) with a minimum stress value of 0.01, and Cluster Analysis. For the latter, distances between clusters were calculated based on average similarity. For transect clusters identified, species discriminating the clusters were analyzed using the Similarity Percentages (SIMPER) module in Primer (Clarke & Gorley 2006). The proportional contribution of the species to the average Bray-Curtis dissimilarity between clusters was calculated (Clarke & Warwick 1994a).

S^{BC} of species assemblages was compared between Invaded and Non-Invaded Transects by using the Analysis of Similarities (ANOSIM) test for replicates from one-way layouts (Clarke & Warwick 1994b) in Primer (Clarke & Gorley 2006) to test for the null hypothesis of no differences between the groups. The R statistic was calculated as a measure of the degree of transect separation. The significance level was then calculated by re-computing the R statistic under permutation of the transect labels, using the maximal number of permutations possible, and referring the observed R value to the permutation distribution of the R value.

Species co-occurrence within the transects was analyzed by testing for non-random patterns of co-occurrence, using the EcoSim package (Gotelli & Entsminger 2010) and presence-absence data. For each transect the Checkerboard Score (C-Score) (Stone & Roberts 1990) was calculated. This index is a quantitative measure of Checkerboard Units found for each species pair, a Checkerboard Unit being the 2x2 submatrix of the form 01 | 10 or 10 | 01. The C-Score gives the average number of checkerboards for each species pair and is compared to a null model. If the observed C-Score (C_{obs}) is comparatively large, there is more segregation than expected, while a comparatively small C-Score indicates more aggregation in the co-occurrence pattern than expected.

Null-model distributions were constructed by means of randomization, using an algorithm in which species occurrences and sample plots are preserved. This randomization algorithm has

a low probability of Type I errors compared to a variety of random data matrices (Gotelli 2000). For each transect, 5000 random matrices were created, for which the C-Score (Simulated C-Score, C_{sim}) was calculated. The Standardized Effect Size (SES) (Gurevitch et al. 1992) was calculated by dividing the difference between C_{obs} and the mean of C_{sim} by the standard deviation of the 5000 simulated indices. In order to test the null-hypothesis that SES did not differ from zero, a single sample t-test was used. Under the assumption of normally distributed deviations, about 95% of the SES values should fall between -2.0 and 2.0. SES was used to decide whether C_{obs} differed significantly (α=0.05) from the mean of C_{sim}, that is, from randomness (Sanders et al. 2003).

Finally, closest distance to a watercourse as well as to a tarred road, a measure of proximity to the urban fringe, were compared between transects with *Li. humile* and transects without this ant by means of unpaired t-test. All t-tests and Mann-Whitney tests were run using GraphPad Prism v5.03 (GraphPad Software 2010). Normality analysis by means of frequency-distribution histograms, Kolmogorov-Smirnov and D'Agostino-Pearson omnibus K2 normality tests was also performed in GraphPad Prism v5.03 (GraphPad Software 2010).

RESULTS

Lycaenidae and food plants

In total, six myrmecophilous species of Lycaenidae were observed at the study site. Except for two individuals of *Al. thyra thyra*, all were males. The most abundant species were *Al. thyra thyra* (25 marked individuals), *Al. pierus* (21) and *Tarucus thespis* (six). Only one individual of *Al. almeida*, *Al. aranda* and *Chrysoritis palmus* was marked. Two individuals of *Al. thyra thyra* were recaptured once, both two days after marking, and the distance between the site of marking and the site of recapture ranged from 10m to 110m. Four individuals of *Al. pierus* were recaptured once, and the distances between site of marking and site of recapture were: 10m (2 days after marking); 20m (3 days after marking); 50m (2 days after marking); and 90m (5 days after marking). *Aspalathus* spp. found in the study area included *As. chenopoda*, *As. cordata*, *As. ericifolia*, *As. lacrifolia*, and *As. sarcodes*. Although being widely distributed across the study area, *Aspalathus* spp. were not found in Transect 7 and Transect 9, both characterized by the highest butterfly activity in the study area.

Ant-Assemblage Composition

The assessment of ant assemblages on the northwestern slopes of the Lion's Head revealed a total absence of *Li. humile* from this region. By far the most abundant ant species was *Lepis. capensis*.

In the main study site above Camps Bay, transects retrieved 2792 indigenous individual ants of 33 species (Appendix 2). In addition, *Li. humile* was found in four transects, varying markedly in occurrence and being most frequent in Transect 4. In Transect 2 and 6 an occurrence of *Li. humile* of only one and two traps out of 24 traps per transect, respectively, were observed, as opposed to 11 and 18 traps collecting *Li. humile* in Transect 1 and 4, respectively. Similarly, one and three individuals of *Li. humile* were collected from Transect 2 and 6, respectively, while 17 and 78 individuals were sampled in Transect 1 and 4, respectively.

Species accumulation curves for the transects reached asymptotes. The observed species richness for all transects ($\bar{x}$=12.8, SD±3.0, N=10) differed significantly from the Incidence-Based Coverage Estimator (ICE) ($\bar{x}$=16.0, SD±4.8, N=10) (P=0.0026, paired t-test), and from

the Chao 2 Richness Estimator (Chao 2) ($\bar{x}$=14.5, SD±4.2, N=10) (P=0.0044, paired t-test). Further, the ICE ($\bar{x}$=16.0, SD±4.8, N=10) differed significantly from Chao 2 ($\bar{x}$=14.5, SD±4.2, N=10) (P=0.0134, paired t-test).

Comparison between Invaded and Non-Invaded Transects with regard to abundance, occurrence, observed species richness and species richness estimators yielded no significant differences at all (Table 1). Generalized Myrmicinae occurred in markedly lower individual numbers in Invaded Transects compared to Non-Invaded. For Subordinate Camponotini, markedly higher abundance and occurrence were observed in Invaded Transects compared to Non-Invaded. *Lepis. capensis* was sampled in markedly lower individual numbers and from fewer traps in Invaded Transects compared to Non-Invaded.

Ant species diversity measured as Exponential Shannon Index (exp(H')) and Simpson-Yule Index (D) varied markedly between the transects (Figure 2). Invaded Transects ranked high in species diversity. However, Invaded Transects did not differ significantly in exp(H') ($\bar{x}$ =10.5, SD±0.6, N=2) compared to Non-Invaded ($\bar{x}$ =7.9, SD±2.6, N=8) (P=0.2155, unpaired t-test). Invaded Transects also did not differ significantly in D ($\bar{x}$=10.0, SD±1.6, N=2) from Non-Invaded ($\bar{x}$=6.5, SD±2.4, N=8) (P=0.0905, unpaired t-test).

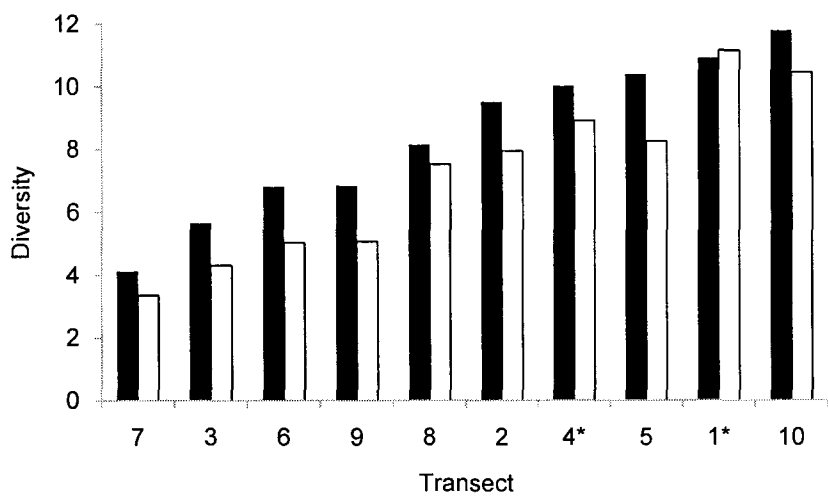

Figure 2. Ant species diversity within transects, ranked according to Exponential Shannon Index (■) and Simpson-Yule Index (□). Ranking differs for Transects 4 and 5 as well as 1 and 10, depending on which index is used. (*) Transects invaded by *Linepithema humile*.

Table 1. Comparison of ant assemblages in Invaded and Non-Invaded Transects. The whole species set, functional groups, and two important Lycaenidae-associated ant species were analyzed.

		Invaded Transects (N=2) Mean±SD	Non-Invaded Transects (N=8) Mean±SD	P	test
All Species					
	Abundance	247.5 ±102.5	287.1 ±112.5	0.6645	t
	S_{obs}	13.5 ± 0.7	12.6 ± 3.4	0.7390	t
	ICE	14.6 ± 1.3	16.3 ± 5.4	0.6858	t
	Chao 2	14.5 ± 1.4	14.5 ± 4.8	0.9943	t
	Occurrence	24.0 ± 0.0	22.4 ± 1.4	0.2021	M
Generalized Myrmicinae (excl. *Monomorium* spp.)					
	Abundance	65.0 ±31.1	118.4 ±54.4	0.2310	t
	S_{obs}	1.5 ± 0.7	1.5 ± 0.8	1.0000	t
	Occurrence	14.0 ± 0.0	18.1 ± 4.2	0.3578	M
Generalized Myrmicinae (incl. *Monomorium* spp.)					
	Abundance	77.0 ±25.5	123.8 ±55.3	0.2930	t
	S_{obs}	3.0 ± 1.4	3.1 ± 1.4	0.9105	t
	Occurrence	16.5 ± 0.7	19.0 ± 3.3	0.3304	t
Opportunists					
	Abundance	99.0 ±58.0	114.3 ±80.7	0.8113	t
	S_{obs}	5.5 ± 2.1	3.9 ± 1.5	0.2231	t
	Occurrence	18.0 ± 5.7	17.4 ± 3.9	0.8537	t
Subordinate Camponotini					
	Abundance	16.0 ±12.7	7.6 ± 9.1	0.3039	t
	S_{obs}	2.5 ± 0.7	2.6 ± 1.7	0.9235	t
	Occurrence	9.0 ± 5.7	4.6 ± 3.9	0.2162	t
Lepisiota capensis					
	Abundance	18.0 ±14.1	74.5 ±77.0	0.3511	t
	Occurrence	6.5 ± 2.1	11.4 ± 6.9	0.3708	t
Pheidole capensis					
	Abundance	45.5 ±58.7	53.5 ±62.6	0.8746	t
	Occurrence	9.0 ± 7.1	8.8 ± 9.4	0.9733	t

Abundance: number of individuals

S_{obs}: observed species richness

ICE: Incidence-Based Coverage Estimator

Chao 2: Chao 2 Richness Estimator

Occurrence: number of traps containing relevant species

t: unpaired t-test

M: Mann-Whitney test

Resemblance of Ant Communities

Analysis of ant community composition by transect using Bray-Curtis similarity (S^{BC}) resulted in the identification of three groups and two separated transects at a resemblance level of 48% (Figure 3). *P. megacephala* and *Lepis. capensis* contributed the most (36.9% and 21.7%, respectively) to transect resemblance within the cluster of Transect 1, 5 and 9. *P. capensis* and *Lepis. capensis* contributed the most (49.0% and 39.1%, respectively) to transect resemblance within the cluster of Transect 3, 6 and 7, whilst transect resemblance within the cluster of Transect 8 and 10 was contributed to most by *P. megacephala* (37.5%), *Tet. capense* (18.8%) and *Rhoptromyrmex* sp. 1 (15.6%). Transect 2 and 4 group together at a similarity level of 42.3%. To transect resemblance within this cluster, the most was contributed by *Tet. sericeiventre* (31.8%), *Tet. regulare* (15.9%) and *P. capensis* (15.9%). Transects did not group together according to presence of or invasion by *Li. humile*. With regard to Bray-Curtis similarity, the null hypothesis of no assemblage differences between Invaded and Non-Invaded Transects could not be rejected at the 5%-significance level (P=0.4000, R=0.034, 45 permutations, analysis of similarities).

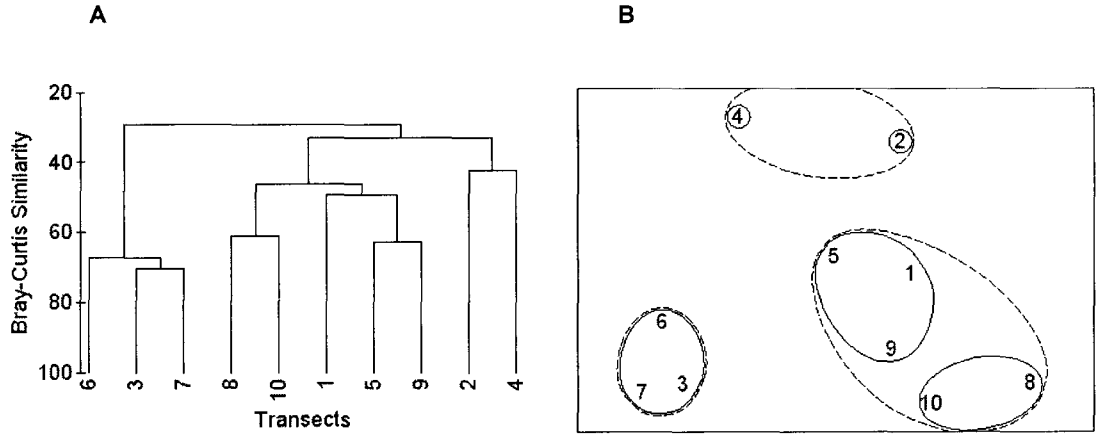

Figure 3. Dendrogram (A) and Non-Metric Multidimensional-Scaling (MDS) plot (B) of the transects (1-10) resulting from resemblance analysis using Bray-Curtis similarity. Continuous line: Grouping based on Bray-Curtis similarity of 40. Dashed line: Grouping based on Bray-Curtis similarity of 48. A stress value of 0.06 was associated with the MDS plot.

Co-occurrence Patterns

The calculation of the Checkerboard Score (C-Score) revealed co-occurrence patterns that did not differ significantly from randomized null models for all transects, except for Transect 8 (Table 2). The observed C-score (C_{obs}) in Transect 8 was significantly larger than the C-Score simulated by the null model (C_{sim}). C_{obs} was greater than C_{sim} for Transects 1, 3, 4, 9 and 10, but not significantly so. C_{obs} was smaller than C_{sim} for Transects 2, 5, 6, and 7, but again the difference was not significant. The 5%-significance level was nearly reached in Transect 1.

Table 2. Analysis of patterns in co-occurrence of species. The Checkerboard Score (C-Score) observed in the transects was compared to a C-Score simulated for randomized matrices.

Transect	*Li. humile* occurrence (traps per transect)	C_{obs}	Csim Mean	Variance	$P(C_{obs} \leq C_{exp})$	$P(C_{obs} \geq C_{exp})$	SES
1	11	13.43590	13.00614	0.05269	0.9570	0.0464	1.87220
2	1	8.34066	8.47024	0.07317	0.3494	0.6678	-0.47902
3	-	4.53333	4.31613	0.14926	0.7870	0.2274	0.56221
4	18	9.20879	9.21955	0.06847	0.5374	0.4810	-0.41110
5	-	6.16176	6.25743	0.03857	0.3492	0.6670	-0.48711
6	2	3.94872	4.26544	0.07528	0.1068	0.9052	-1.15434
7	-	6.57143	6.86635	0.39279	0.3976	0.6420	-0.47058
8	-	9.74545	8.73157	0.08380	0.9952	0.0048	3.50239*
9	-	4.83333	4.65250	0.02809	0.8682	0.1482	1.07902
10	-	5.40441	5.37617	0.02529	0.6052	0.4082	0.17760

*significantly different from null model

C_{obs}: observed Checkerboard Score

C_{sim}: simulated Checkerboard Score

C_{exp}: expected Checkerboard Score = Mean of C_{sim}

SES: Standardized Effect Size

Environmental Factors

Transects varied markedly in distance to tarred road and distance to nearest watercourse (Figure 4). Transect 2 and 6 were situated closest to a watercourse, while Transect 4 was closest to a tarred road. Transect 1 was the second-furthest from a watercourse, but relatively close to a tarred road. With regard to distance to a watercourse no significant differences were found between transects with *Li. humile* ($\bar{x}$=162.5m, SD±132.8m, N=4) and transects without this ant ($\bar{x}$=276.7m, SD±86.9m, N=6) (P=0.1353, unpaired t-test). Transects with *Li. humile* did not differ significantly in proximity to a tarred road ($\bar{x}$=205.0m, SD±100.2m,

N=4) compared to transects free of *Li. humile* ($\bar{x}$=386.7m, SD±166.5, N=6) (P=0.0886, unpaired t-test). Transects with *Li. humile* were markedly closer to watercourses and tarred roads.

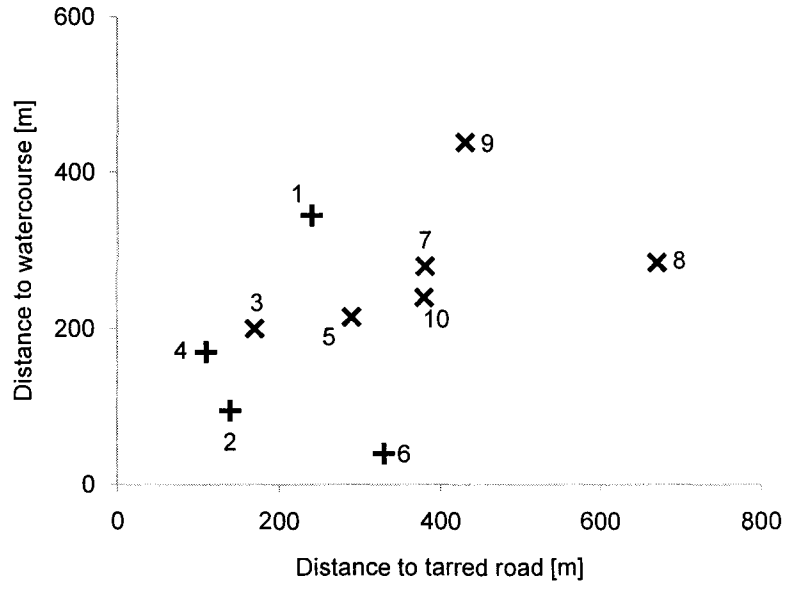

Figure 4. Environmental factors recorded for the transects (1-10). (+) Transects with *Linepithema humile*. (x) Transects without *Li. humile*.

DISCUSSION

Status of *Li. humile* in the study area

Overall, the study area seems to be only weakly invaded by *Li. humile*. The ant species appears to be patchily distributed in the study area, being present in only four out of 10 transects. Patchy distributions of *Li. humile* have been observed in previous studies (Ward 1987). On the other hand, the probability of detection of *Li. humile* using unbaited pitfall traps was relatively low for a sampling period of one week (P=0.48) compared to longer sampling periods (Stanley et al. 2008). Thus, in the present study presence of *Li. humile* is likely to be underestimated. The relatively low occurrence of *Li. humile* in the study area is further in accordance with earlier observations that *Li. humile* seems to avoid pristine Fynbos (Pryke & Samways 2010). In terms of occurrence, *Li. humile* was identified as the dominant ant species only in one transect. The very low occurrences of *Li. humile* in two other transects might relate to small satellite colonies that are not established (Human & Gordon 1996).

As the present study provides only a snapshot in time, the invasion dynamics of *Li. humile* in the longer term remain obscure. Bolger (2007) observed great annual fluctuations in abundance of *Li. humile* close to the urban fringe. Moreover, the distribution of *Li. humile* colonies undergoes seasonal changes. In northern California, where climatic conditions are similar to the Western Cape, the colony network of *Li. humile* expands during spring and summer and contracts during autumn and winter (Heller & Gordon 2006). Correspondingly, the distribution undergoes expansion in summer and contraction in winter (Sanders et al. 2001; Heller et al. 2006). Likewise, *Li. humile* appears to enter homes in search of a favorable environment under cool and wet conditions (Gordon et al. 2001). Thus, it appears that ant sampling for the present study occurred at a time when *Li. humile* distribution in the study area may not have been at its maximum. The invasion front of *Li. humile* spreads at a typical rate of 100m per year (Erickson 1971; Holway 1995), with occasional jump dispersal over much longer distances (Holway 1995), while the spread of *Li. humile* from established colonies behind the invasion front occurs at expected rates of 66m per year (Heller et al. 2006). Even under the conservative assumption that *Li. humile* distribution within the study area was still at its maximal seasonal contraction, transects without observed presence of *Li. humile* are probably not affected by *Li. humile* immigration in the course of seasonal distribution shifts, as the transects were set up several hundred meters apart from each other.

The study area is adjacent to the urban fringe of Camps Bay. *Linepithema humile* is known to invade fragments of natural habitat from the urban fringe (Suarez et al. 1998), and the same is true for large areas of natural habitat (Bolger 2007). *Linepithema humile* invasion of coastal sage scrub in southern California is restricted to distances of about 200m in habitat fragments (Suarez et al. 1998) and rarely proceeds further than 250m from the urban edge in large areas of natural habitat (Bolger 2007). Accepting proximity to the nearest tarred road as a measure of proximity to the urban fringe, the presence of *Li. humile* could be detected as far as 330m from the urban fringe. The Invaded Transects are situated at distances to the urban fringe that compare well with the observations of Suarez et al. (1998) and Bolger (2007). Moreover, *Li. humile* is spreading into fire breaks within fynbos vegetation (De Kock 1983). The firebreaks separating Camps Bay from the natural Fynbos vegetation might be attributed to the urban area, in which case distances of transects with *Li. humile* to the urban fringe would become markedly smaller. The latter would also be the case if distance to the closest building, which has been suggested as best predictor for the occurrence of *Li. humile* (Human et al. 1998), was used as a measure of distance to the urban fringe. Finally, the virtual absence of nearby buildings on Lion's Head could explain the complete absence of *Li. humile* from this pilot-study area.

Water availability seems to be an important factor determining invasibility of natural habitat with regard to *Li. humile* and could also explain the absence of this ant from the sampled area on Lion's Head. Areas of high humidity are preferred by *Li. humile* (Walters & Mackay 2003a; Heller & Gordon 2006), and annual fluctuation in abundance of *Li. humile* near the urban fringe was positively related to annual rainfall (Bolger 2007). The Western Cape has very low summer rainfall, which might be the limiting factor for the spread of *Li. humile* into natural vegetation lacking a permanent water source.

Urban water runoff, though not a prerequisite for the invasion of *Li. humile* into natural habitat (Bolger 2007), has been considered important in determining habitat invasibility to *Li. humile* (Suarez et al. 1998). Habitat fragments downslope from urban areas were characterized by a higher abundance of *Li. humile* than upslope habitat fragments (Holway et al. 2002b). The study area is situated upslope from the Camps Bay residential area, and the lack of urban runoff could be a reason for their low occurrence in the study area.

Soil-type heterogeneity could be a factor determining distribution of *Li. humile* in the study area. Drainage of soils predicted the extent of invasion by *Li. humile* in southern California,

with soils retaining more moisture supporting greater spatial penetration and higher abundances of *Li. humile* than well-drained soils (Bolger 2007). In laboratory experiments, survival of *Li. humile* workers was depressed at low levels of soil moisture (Holway et al. 2002b). In field experiments, abundance of *Li. humile* increased locally under drip irrigation, increased plant growth only partly explaining the increase (Menke & Holway 2006). However, soil analysis was out of the scope of this study.

In coastal sage scrub of southern California *Li. humile* is largely confined to areas with permanent water availability (Ward 1987). The ant reaches highest abundance within moist riparian corridors while its abundance decreases sharply with increasing distance to the corridors (Holway 2005). On the other hand, distance to surface water appeared less important in determining the spread of invasion by *Li. humile* than proximity to disturbed areas (Human et al. 1998). The present study did not find significant difference in mean distance to the nearest watercourse between Invaded and Non-Invaded Transects. Seasonally intermittent watercourses in southern Californian sage scrub are generally not invaded by *Li. humile* (Ward 1987), and the non-perennial watercourses in the study area do not seem to be of primary importance for the invasibility of the area.

In addition to water availability and urban areas, invasibility to *Li. humile* is further determined by temperature limitations (Silverman & Brightwell 2008). *Li. humile* individuals do not survive temperatures of above 46°C for longer than one hour (Holway et al. 2002b). Further, workers of *Li. humile* showed maximal abundance at baits at 34.0°C and stopped foraging at 41.6°C (Holway et al. 2002b). As there are no temperature data available for the study area, the role of temperature in determining the distribution of *Li. humile* in the study area could not be assessed. Nonetheless, both temperature and humidity might help explain the low occurrence of *Li. humile* in the study site. Fynbos on the western and northern slopes of Table Mountain is drier and hotter compared to the southern and eastern slopes (Pryke & Samways 2010).

Lastly, the extent of roads is another variable explaining the successful establishment of introduced species (Borges et al. 2006). In South African fynbos, presence of *Li. humile* is typically dependent on vehicular access to the area in general, and connection of the area to tarred roads in particular (De Kock & Giliomee 1989). The distance of Invaded Transects to the nearest tarred road was not significantly shorter compared to Non-Invaded Transects, thus proximity to tarred roads does not seem to play an important role in determining the spread of

invasion in the study area. It should be noted that the study area is in great parts accessible to vehicles, but this access is restricted to official authorities. However, even this restricted vehicular access, although not to the same extent as gravel- or tarred roads open to the public, is a factor determining a habitat's susceptibility to invasion through *Li. humile* (De Kock & Giliomee 1989), and could confound the results for the proximity of transects to tarred roads obtained in the present study.

Impact of *Li. humile* on native ant species assemblages

The invading *Li. humile* displaces native epigeic ants (Skaife 1962; Ward 1987; Carpintero et al. 2004; Rowles & O'Dowd 2009a). However, in the present study observed species richness and richness estimators were not significantly lower in Invaded Transects compared to Non-Invaded. Moreover, there was a considerable variation in observed and estimated species richness among Non-Invaded Transects. This indicates that factors other than invasion by *Li. humile* play an important role in determining species richness in the study area.

Unexpectedly, ant communities of Invaded Transects were not different to those of Non-Invaded Transects. *Linepithema humile* appears not to have impacted on the ant species observed in the study area to a great extent. *Lepisiota capensis* did not have significantly lower abundances and occurrences in Invaded Transects compared to Non-Invaded. The abundances of *Li. humile* might probably be not high enough to change the native ant community composition of Invaded Transects. Furthermore, native ant species can temporarily persist at the invasion front of *Li. humile* (Human & Gordon 1996), and the study area above Camps Bay might coincide with the invasion front of *Li. humile*.

A considerable degree of variation was observed with respect to diversity indices among Transects, and there were no significant differences between the two diversity indices for Invaded and Non-Invaded Transects. Also, transects with *Li. humile* did not differ significantly in species diversity from transects without this ant. Thus, *Li. humile* presence does not seem to be important for species diversity of ant communities in the study area. In contrast, other studies have found that ant species diversity in montane Fynbos is lower under presence of *Li. humile* than in absence of the ant (Donnelly & Giliomee 1985), while β-diversity in particular has been reported to be reduced in areas invaded by *Li. humile* (Holway & Suarez 2006).

The functional-group approach based on responses to environmental stress and disturbance on a global scale, though not designed for the analysis of local-scale community dynamics, offers a useful framework for studies concerning the broad structure of particular communities (Andersen 2010). No significant difference was found with regard to density of Generalized Myrmiciniae in Invaded Transects compared to Non-Invaded, as indicated by corresponding individual numbers. The assessment of density based on individual numbers from pitfall traps has been criticized (Veile 1991). Using individual numbers in community studies of social insects is often misleading due to their aggregative nature (Longino 2000) and coloniality. Social behavior such as mass recruitment by trapped individuals likely bias density assessment based on abundance of individuals (Seifert 1990). However, results for occurrence are in accordance with the findings based on individual numbers.

Ant species in this functional group have a relatively broad distribution with regard to environmental stress compared to the Dominant Dolichoderinae (Andersen 1995), to which *Li. humile* belongs (Andersen 2010). Thus, Non-Invaded Transects might be characterized by a stress or disturbance regime that prevents *Li. humile* from establishing but is suitable for *Pheidole* and *Monomorium* spp. Despite larger foraging ranges and colony sizes as well as higher levels of individual activity and aggression (Andersen 1995, 2010), *Li. humile*, due to its low abundance, might not be able to depress occurrences of Generalized Myrmicinae within Invaded Transects.

No significant differences in abundance and occurrence between Invaded and Non-Invaded Transects were found for *P. capensis*, which is in contrast to previous findings. A markedly reduced abundance of *P. capensis* in Fynbos areas invaded by *Li. humile* compared to non-invaded areas was observed by Donnelly & Giliomee (1985), probably accompanied by a corresponding occurrence. Another study indicated the absence of *P. capensis* from Fynbos areas invaded by *Li. humile* (Bond & Slingsby 1984), while the present study recorded the presence of *P. capensis* in all transects with *Li. humile* presence. However, the previous work drew conclusions about species distributions based on surveys at baits (Bond & Slingsby 1984), which are useful in assessing the distribution of *Li. humile*, but are not sufficient for the assessment of native ant species (Casellas et al. 2009).

The coexistence of *P. megacephala* with *Li. humile* in the study area is in accordance with previous observations that *Li. humile* does not displace *P. megacephala* (Erickson 1971). Replacement of *Li. humile* by *P. megacephala*, as observed at some locations in Bermuda

(Haskins & Haskins 1988), cannot be confirmed by the present data, although there are four transects not invaded by *Li. humile* with relatively high occurrence of *P. megacephala.*

By definition Opportunists occur typically at sites under stress or disturbance where they can escape competition from other ant species (Andersen 1995). There was no marked difference in observed species richness, occurrence, and abundance of Opportunists between Invaded and Non-Invaded Transects. In particular, abundance and occurrence of *Lepis. capensis* did not differ significantly between Invaded and Non-Invaded Transects. This species was not observed to coexist with *Li. humile* in the Fynbos (Slingsby 1982; Donnelly & Giliomee 1985). Occurrence of *Li. humile* in invaded sites within the study area might be low enough to allow for the coexistence with Opportunists. Cryptic nature and low abundance of some indigenous ants were suggested as potentially explaining their coexistence with *Li. humile* (De Kock 1990).

Occurrence and abundance of *Camponotus* species, which are the only representatives of the Subordinate Camponotini in the study area, do not appear to be significantly different in Invaded Transects compared to Non-Invaded. This seems to contradict earlier findings that abundance of *Camponotus* species is markedly reduced in Fynbos sites invaded by *Li. humile* compared to non-invaded sites (Donnelly & Giliomee 1985). However, Subordinate Camponotini often coexist with Dominant Dolichoderinae (Andersen & Patel 1994). Submissive behavior and, in most species, nocturnal foraging of *Camponotus* spp. are apparent reasons for their successful coexistence with the Dominant Dolichoderinae (Andersen & Patel 1994).

The ability of *Meranoplus peringueyi* to coexist with *Li. humile* (De Kock 1990) seems to be in congruence with the present study. No *Anoplolepis* species were found in the study site. *Anoplolepis custodiens,* one of the dominant ant species in the Fynbos (De Kock 1990), is usually displaced by *Li. humile* (Slingsby 1982; Donnelly & Giliomee 1985; De Kock 1990). The complete absence of the former from the study area could indicate a more widespread impact of *Li. humile* on ant communities than is obvious from the short observation of this study.

Only for the Non-Invaded Transect 8 was a co-occurrence pattern observed that significantly differed from randomness. An observed C-Score greater than the simulated indicates that there is less species co-occurrence than expected (Stone & Roberts 1990), and thus the

assemblage in this transect seems to be dominated by avoidance between species. As expected, all Invaded Transects appear to have a random pattern of species co-occurrence. Ant communities invaded by *Li. humile* undergo a rapid change in co-occurrence pattern, from segregated to random or weakly aggregated species co-occurrences (Sanders et al. 2003). In contrast to these findings, all the Non-Invaded Transects, except for Transect 8, do not show indications of species segregation. Moreover, the co-occurrence pattern in Invaded Transect 1, which is almost deviating at a significant level from randomness, indicates a weak segregation rather than aggregation of species. However, as co-occurrence data prior to the introduction of *Li. humile* are unknown, the observed co-occurrence pattern cannot be attributed to the invasion.

The C-Score method based on presence-absence data has been criticized for being too conservative, as differences in abundance at shared sites are not accounted for (Blüthgen & Stork 2007). However, as discussed above, incidence may be preferred over abundance in studies on social insects. Random co-occurence patterns in Non-Invaded Transects might indicate the temporal penetration of these transects by *Li. humile* under more favorable conditions, e.g. during wetter seasons or years. This is further indicated by the fact that the only transect with non-random co-occurrence pattern is situated furthest from the urban edge, from where *Li. humile* invasions usually spread (Suarez et al. 1998; Bolger 2007).

Impact of *Li. humile* on ant-butterfly associations

Myrmecophilous species of Lycaenidae recorded from the study area, their ant associations as well as flight periods are listed in Appendix 1. *Thestor yildizae*, which has been recorded to occur on the Twelve Apostles, was not recorded because the sampling period did not overlap with the flight period of this butterfly species (Claassens & Dickson 1980). However, it is questionable whether *Th. yildizae* is breeding in the study area, as the obligatorily associated ant *Ano. custodiens* seems to be absent from the study area.

Chrysoritis palmus palmus, which was not recorded to occur in the region around the study area and which was encountered only once, is probably not breeding in the study area as the ant genus *Crematogaster*, with which *Ch. palmus palmus* is obligatorily associated (Claassens 2000), appears to be absent from the study area. The absence of *Crematogaster* spp. from the study area could not only help explain the low abundance of *Ch. palmus palmus*, but also the apparent absence of *Ch. zeuxo* from the study area. However, the

observed absence of *Crematogaster* spp. could be explained by the arboreal life style of these ants. Donnelly & Giliomee (1985) found no *Crematogaster* spp. in their pitfalls, although these ant species were known from the sampling area.

The fairly high numbers of *Al. thyra* and *Al. pierus* are congruent with the high occurrence of their obligatorily associated ant species, *Lepis. capensis*. Not only are these butterfly species dependent on *Lepis. capensis* to complete their life cycle, but the nutritive secretions from the honey glands of lepidopteran larvae most likely benefit the colonies of their associated ant species (Fiedler & Saam 1995). The apparent absence of *Anthene definita definita* and the low encounter rate of *Al. aranda* can neither be explained by their flight period nor by means of their associated ants, which occur quite often in the study area. These findings emphasize that the presence of strongly associated ant species are a prerequisite for the occurrence of myrmecophilous Lycaenidae, but only one among several factors, such as larval food plants, underlying the distribution of these butterflies. The relatively low occurrence of *Camponotus* species in the study area could contribute to the apparent absence of *Lepidochrysops* species. However, there is no information about frequencies of associated ants in areas occupied by *Lepidochrysops* species. In any event, different species would be expected to have different abundances for a host of other reasons.

The study shows that for *Al. pierus* and *Al. thyra thyra*, and probably for other myrmecophilous Lycaenidae, scoring of imagines alone is insufficient for assessing the impact of *Li. humile* invasion on associations between native ants and Lycaenidae. Male *Al. pierus* and *Al. thyra thyra* imagines, which accounted for the majority of butterflies observed in this study, showed territorial behavior and were remarkably sedentary, confirming earlier observations (Dickson & Kroon 1978). However, because of the lack of *Aspalathus* spp., which contain the larval food plants of *Al. thyra thyra* and *Al. pierus* (Dickson 1953; Claassens 2000), in transects with the highest abundance of these butterflies, males must have migrated from the site of larval development to their territories where they were observed. Thus, while indications about impacts can be gained by analyzing host ant density, scoring of butterfly larvae appears to be necessary to assess direct impacts of *Li. humile* on associations between the two *Aloeides* species and their native host ants.

SYNTHESIS

From the findings of the present study it seems that *Linepithema humile* has only minor effects on the native ant community of the slopes of Table Mountain above Camps Bay, with little consequences for ecosystem processes in the area. This is an interesting finding for an area adjacent to the urban fringe, given that much greater impacts have been observed at natural Fynbos sites much less affected by urbanization, such as the Kogelberg area (Bond & Slingsby 1984) and Jonkershoek valley (Donnelly & Giliomee 1985). While the interplay of the abiotic environment and native biota shapes the invasibility of habitats (Holway 1998; Menke et al. 2007), the role of disturbance regimes in governing invasion processes has been stressed by Kruger et al. (1989).

The present results suggest that, at least in terms of *L. humile* invasion, edges can contribute to overall conservational value of protected areas to a similar degree as do core areas. This could raise optimism, because on the Cape Peninsula the edges of protected areas often contain patches of low-lying habitat types that are generally under-represented in nature reserves (Holmes et al. 2008), and edge effects are generally thought to reduce the conservational value of peripheral protected areas (Yahner 1988; Donovan et al. 1997).

However, the study provides only a snapshot in time. Impacts of *L. humile* might be more severe in other seasons (Heller & Gordon 2006) and subject to inter-annual variation (Sanders et al. 2001), and the short period of observation underlying this study might result in underestimation of longer-term effects of the invasion. To the knowledge of the author, despite a long history of *L. humile* research in South Africa (Skaife 1961, 1962), there are no studies using fine-scale sampling to observe patterns of invasion into the Fynbos over several years. A high level of myrmecochory and a great diversity in plants depending on it (Bond & Breytenbach 1985; Bond et al. 1990), as well as a high degree of invertebrate endemism (Picker & Samways 1996) would clearly justify investment in the acquisition of this knowledge, which would help in evaluating the status of protected areas on the Cape Peninsula with regard to conservation of fundamental ecosystem processes, and in developing management strategies against the further spread of *L. humile.*

The apparent dispersal of *Aloeides* spp. after completion of their juvenile stages of ontogenesis, which was observed at the study site and is probably similar to the behavior of other myrmecophilous Lycaenidae, discounts the use of imagines for assessing habitat suitability for ant-associated butterflies with regard to ant-assemblage composition at the

local level. Further studies in this direction should consider counts of larvae, although this is much more time-consuming than scoring adult butterflies and probably limits the scope of the study to a few species of interest. Moreover, the apparent lack of empirical knowledge about dispersal in the South African Lycaenidae has to be addressed by conservation biologists in the near future. Mark-recapture techniques should be used to investigate dispersal and meta-population structure in the Lycaenidae of conservational concern across the Cape Peninsula, and ultimately to assess their ability to persist within a disintegrating network of primarily montane Fynbos islands within an expanding matrix of urban areas in the longer term.

REFERENCES

Adamson, R. S., and T. M. Salter 1950. Flora of the Cape Peninsula. Juta, Cape Town.

Addison, P., and M. J. Samways. 2000. A survey of ants (Hymenoptera : Formicidae) that forage in vineyards in the Western Cape Province, South Africa. African Entomology **8**:251-260.

Agrawal, A. A., and J. A. Fordyce. 2000. Induced indirect defence in a lycaenid-ant association: the regulation of a resource in a mutualism. Proceedings of the Royal Society of London Series B-Biological Sciences **267**:1857-1861.

Andersen, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography **22**:15-29.

Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography **24**:433-460.

Andersen, A. N. 2010. Functional groups in ant community ecology. Pages 142-144 in L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant Ecology. Oxford University Press, Oxford.

Andersen, A. N., and A. D. Patel. 1994. Meat ants as dominant members of Australian ant communities - An experimental test of their influence on the foraging success and forager abundance of other species. Oecologia **98**:15-24.

Atsatt, P. R. 1981. Ant-dependent food plant-selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). Oecologia **48**:60-63.

Blancafort, X., and C. Gomez. 2005. Consequences of the Argentine ant, *Linepithema humile* (Mayr), invasion on pollination of *Euphorbia characias* (L.) (Euphorbiaceae). Acta Oecologica-International Journal of Ecology **28**:49-55.

Blancafort, X., and C. Gomez. 2006. Downfall of pollen carriage by ants after Argentine ant invasion in two Mediterranean *Euphorbia* species. Vie Et Milieu-Life and Environment **56**:243-246.

Blüthgen, N., and N. E. Stork. 2007. Ant mosaics in a tropical rainforest in Australia and elsewhere: A critical review. Austral Ecology **32**:93-104.

Bolger, D. T. 2007. Spatial and temporal variation in the Argentine ant edge effect: Implications for the mechanism of edge limitation. Biological Conservation **136**:295-305.

Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press, Cambridge.

Bond, W., and P. Slingsby. 1984. Collapse of an ant-plant mutalism: The Argentine ant (*Iridomyrmex humilis*) and Myrmecochorous Proteaceae. Ecology **65**:1031-1037.

Bond, W. J., and G. J. Breytenbach. 1985. Ants, rodents and seed predation in Proteaceae. South African Journal of Zoology **20**:150-154.

Bond, W. J., R. Yeaton, and W. D. Stock. 1990. Myrmecochory in Cape fynbos. Pages 448-462 in C. R. Huxley, and D. F. Cutler, editors. Ant-plant interactions. Oxford University Press.

Boonzaaier, C., M. A. McGeoch, and C. L. Parr. 2007. Fine-scale temporal and spatial dynamics of epigaeic ants in Fynbos: sampling implications. African Entomology **15**:1-11.

Borges, P. A. V., J. M. Lobo, E. B. de Azevedo, C. S. Gaspar, C. Melo, and L. V. Nunes. 2006. Invasibility and species richness of island endemic arthropods: a general model of endemic vs. exotic species. Journal of Biogeography **33**:169-187.

Buczkowski, G., and G. W. Bennett. 2008a. Aggressive interactions between the introduced Argentine ant, *Linepithema humile* and the native odorous house ant, *Tapinoma sessile*. Biological Invasions **10**:1001-1011.

Buczkowski, G., and G. W. Bennett. 2008b. Detrimental effects of highly efficient interference competition: Invasive Argentine ants outcompete native ants at toxic baits. Environmental Entomology **37**:741-747.

Buczkowski, G., R. Kumar, S. L. Suib, and J. Silverman. 2005. Diet-related modification of cuticular hydrocarbon profiles of the Argentine ant, *Linepithema humile*, diminishes intercolony aggression. Journal of Chemical Ecology **31**:829-843.

Carpintero, S., J. Retana, X. Cerda, J. Reyes-Lopez, and L. A. De Reyna. 2007. Exploitative strategies of the invasive Argentine ant (*Linepithema humile*) and native ant species in a southern Spanish pine forest. Environmental Entomology **36**:1100-1111.

Carpintero, S., and J. Reyes-Lopez. 2008. The role of competitive dominance in the invasive ability of the Argentine ant (*Linepithema humile*). Biological Invasions **10**:25-35.

Carpintero, S., J. Reyes-Lopez, and L. A. de Reyna. 2004. Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. Biological Conservation **115**:279-289.

Carpintero, S., J. Reyes-Lopez, and L. A. De Reyna. 2005. Impact of Argentine ants (*Linepithema humile*) on an arboreal ant community in Doñana National Park, Spain. Biodiversity and Conservation **14**:151-163.

Casellas, D., C. Gomez, and M. Clavero. 2009. Comparing methods of evaluating the spread of Argentine ants in natural habitats: Pitfall traps vs. baiting. Sociobiology **53**:927-938.

Chao, A. 1987. Estimating the population-size for capture recapture data with unequal catchability. Biometrics **43**:783-791.

Chazdon, R. L., R. K. Colwell, J. S. Denslow, and M. R. Guariguata. 1998. Species richness of woody regeneration in primary and secondary rainforests of northeastern Costa Rica. in F. Dallmeier, and J. A. Comiskey, editors. Forest biodiversity research, monitoring and modelling: Conceptual background and Old World case studies. Pathenon, Paris.

Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature **413**:635-639.

Claassens, A. J. M. 1976. Observations on the myrmecophilous relationships and the parasites of *Lepidochrysops methymna methymna* (Trimen) and *L. trimeni* (Bethune-Bake) (Lepidoptera: Lycaenidae). Journal of the Entomological Society of Southern Africa **39**:279-289.

Claassens, A. J. M. 1991. The mystery of the squeaking pupae of myrmecophilous Lycaenidae. Metamorphosis **2**:19-20.

Claassens, A. J. M. 2000. Butterflies of the Cape Peninsula. Tafelberg Publishers, Cape Town.

Claassens, A. J. M., and C. G. C. Dickson. 1974. The early stages of *Aloeides thyra* (L.) (Lepidoptera: Lycaenidae) with notes on ant association, distribution and general ecology of the species. Entomologist's Record and Journal of Variation **86**:253-258.

Claassens, A. J. M., and C. G. C. Dickson 1980. The butterflies of the Table Mountain Range: With comprehensive observations on their habits, times of appearance and life-histories. Struik, Cape Town.

Clark, G. C., and C. G. C. Dickson. 1956. The honey gland and tubercles of larvae of the Lycaenidae. Lepidopterists' News **10**:37-43.

Clark, G. C., and C. G. C. Dickson 1971. Life histories of the South African lycaenid butterflies. Purnell, Cape Town.

Clarke, K. R., and R. N. Gorley 2006. PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth.

Clarke, K. R., and R. M. Warwick. 1994a. Species analysis in K. R. Clarke, and R. M. Warwick, editors. Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

Clarke, K. R., and R. M. Warwick. 1994b. Testing for differences between groups of samples in K. R. Clarke, and R. M. Warwick, editors. Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

Colwell, R. K. 2006. EstimateS:Statistical estimation of species richness and shared species from samples. Version 8. Accessed at http://viceroy.eeb.uconn.edu/estimates on 12 December 2010.

Cottrell, C. B. 1984. Aphytophagy in butterflies - Its relationship to myrmecophily. Zoological Journal of the Linnean Society **80**:1-57.

d'Ettorre, P., and A. Lenoir. 2010. Nestmate recognition. Pages 194-209 in L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant ecology. Oxford University Press, Oxford.

Deacon, J. 1986. Human settlement in South Africa and archaeological evidence for alien plants and animals. Pages 3-20 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town.

De Kock, A. E. 1983. Monitor vir die teenwoordigheid van die Argentynse mier *Iridomyrmex humilis* in die fynbos van die Jonkershoekvallei. B. Sc. (Hons.) report. University of Stellenbosch, Stellenbosch.

De Kock, A. E. 1990. Interactions between the introduced Argentine ant, *Iridomyrmex humilis* (Mayr), and 2 indigenous Fynbos ant species. Journal of the Entomological Society of Southern Africa **53**:107-108.

De Kock, A. E., and J. H. Giliomee. 1989. A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera, Formicidae) in South-African Fynbos. Journal of the Entomological Society of Southern Africa **52**:157-164.

DeVries, P. J. 1991. Call production by myrmecophilous riodinid and lycaenid Butterfly caterpillars (Lepidoptera). Morphological, acoustical, functional and evolutionary patterns. American Museum Novitates:1-23.

Dickson, C. G. C. 1944. The life-history of *Cupido thespis* (L.) (Lepidoptera: Lycaenidae). Journal of the Entomological Society of Southern Africa 7:20-29.

Dickson, C. G. C. 1953. Recently observed food-plants of some Cape lepidopterous larvae (4th series). Journal of the Entomological Society of Southern Africa **16**:73-76.

Dickson, C. G. C., and D. M. Kroon 1978. Pennington's butterflies of southern Africa. Ad. Donker, Johannesburg.

DiGirolamo, L. A., and L. R. Fox. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). Biological Invasions **8**:125-135.

Donnelly, D., and J. H. Giliomee. 1985. Community structure of epigaeic ants (Hymenoptera, Formicidae) in Fynbos vegetation in the Jonkershoek-Valley. Journal of the Entomological Society of Southern Africa **48**:247-257.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. Ecology **78**:2064-2075.

Erickson, J. M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex Humilis* Mayr. Psyche **78**:257-266.

Fiedler, K., and C. Saam. 1995. Ants Benefit from attending facultatively myrmecophilous Lycaenidae caterpillars - Evidence from a survival study. Oecologia **104**:316-322.

Forsyth, G. G., and B. W. van Wilgen. 2008. The recent fire history of the Table Mountain National Park and implications for fire management. Koedoe **50**:3-9.

Giraud, T., J. S. Pedersen, and L. Keller. 2002. Evolution of supercolonies: The Argentine ants of southern Europe. Proceedings of the National Academy of Sciences of the United States of America **99**:6075-6079.

Glenn, S., and D. Holway. 2008. Consumption of introduced prey by native predators: Argentine ants and pit-building ant lions. Biological Invasions **10**:273-280.

Google Inc. 2007. Google Earth Version 4.2.0205.5730. Google Inc., Mountain View. Accessed at http://www.google.com/intl/en/earth/index.html on 27 December 2010.

Gordon, D. M., L. Moses, M. Falkovitz-Halpern, and E. H. Wong. 2001. Effect of weather on infestation of buildings by the invasive Argentine ant, *Linepithema humile* (Hymenoptera : Formicidae). American Midland Naturalist **146**:321-328.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology **81**:2606-2621.

Gotelli, N. J., and G. L. Entsminger 2010. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho. Accessed at http://garyentsminger.com/ecosim.htm on 12 December 2010.

GraphPad Software 2010. GraphPad Prism version 5.03 for Windows. GraphPad Software, San Diego.

Greene, M. J., and D. M. Gordon. 2007. Structural complexity of chemical recognition cues affects the perception of group membership in the ants *Linephithema humile* and *Aphaenogaster cockerelli*. Journal of Experimental Biology **210**:897-905.

Greenslade, P. J. M. 1973. Sampling ants with pitfall traps - Digging-in effects. Insectes Sociaux **20**:343-353.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Naturalist **140**:539-572.

Haskins, C. P., and E. F. Haskins. 1988. Final observations on *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda. Psyche **95**:177-184.

Heath, A., and A. J. M. Claassens. 2000. New observations on ant associations and life history adaptations (Lepidoptera: Lycaenidae) in South Africa. Metamorphosis **11**:3-19.

Heath, A., and A. J. M. Claassens. 2003. Ant-association among southern African Lycaenidae. Journal of the Lepidopterists' Society **57**:1-16.

Heller, N. E., and D. M. Gordon. 2006. Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). Ecological Entomology **31**:499-510.

Heller, N. E., K. K. Ingram, and D. M. Gordon. 2008a. Nest connectivity and colony structure in unicolonial Argentine ants. Insectes Sociaux **55**:397-403.

Heller, N. E., N. J. Sanders, and D. M. Gordon. 2006. Linking temporal and spatial scales in the study of an Argentine ant invasion. Biological Invasions **8**:501-507.

Heller, N. E., N. J. Sanders, J. W. Shors, and D. M. Gordon. 2008b. Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant. Oecologia **155**:385-395.

Henning, G. A., and S. F. Henning 1989. South African red data book: Butterflies. South African National Scientific Programmes Report No 158. CSIR, Pretoria.

Henning, S. F. 1983a. Biological groups within the Lycaenidae (Lepidoptera). Journal of the Entomological Society of Southern Africa **46**:65-85.

Henning, S. F. 1983b. Chemical communication between lycaenid larvae (Lepidoptera, Lycaenidae) and ants (Hymenoptera, Formicidae). Journal of the Entomological Society of Southern Africa **46**:341-366.

Hirata, M., O. Hasegawa, T. Toita, and S. Higashi. 2008. Genetic relationships among populations of the Argentine ant *Linepithema humile* introduced into Japan. Ecological Research **23**:883-888.

Hölldobler, B., and E. O. Wilson 1990. The ants. Springer, Berlin.

Holmes, P., J. Wood, and C. Dorse. 2008. Cape Town's biodiversity. Pages 10-35 in P. Holmes, J. Wood, and C. Dorse, editors. City of Cape Town biodiversity report 2008. City of Cape Town, Cape Town.

Holway, D. A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in northern California. Conservation Biology **9**:1634-1637.

Holway, D. A. 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia **115**:206-212.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology **80**:238-251.

Holway, D. A. 2005. Edge effects of an invasive species across a natural ecological boundary. Biological Conservation **121**:561-567.

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002a. The causes and consequences of ant invasions. Annual Review of Ecology and Systematics **33**:181-233.

Holway, D. A., and A. V. Suarez. 2004. Colony-structure variation and interspecific competitive ability in the invasive Argentine ant. Oecologia **138**:216-222.

Holway, D. A., and A. V. Suarez. 2006. Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion. Biological Conservation **127**:319-326.

Holway, D. A., A. V. Suarez, and T. J. Case. 2002b. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. Ecology **83**:1610-1619.

Human, K. G., and D. M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia **105**:405-412.

Human, K. G., and D. M. Gordon. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. Conservation Biology **11**:1242-1248.

Human, K. G., S. Weiss, A. Weiss, B. Sandler, and D. M. Gordon. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera : Formicidae). Environmental Entomology **27**:822-833.

Inouye, B. D., and A. A. Agrawal. 2004. Ant mutualists alter the composition and attack rate of the parasitoid community for the gall wasp *Disholcaspis eldoradensis* (Cynipidae). Ecological Entomology **29**:692-696.

IUCN 2010. IUCN red list of threatened species. Version 2010.4. Accessed at http://www.iucnredlist.org on 22 January 2011.

Jordano, D., J. Rodriguez, C. D. Thomas, and J. F. Haeger. 1992. The distribution and density of a lycaenid butterfly in relation to *Lasius* ants. Oecologia **91**:439-446.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology **88**:2427-2439.

Kemp, D. J., and M. P. Zalucki. 1999. Method of handling affects post-capture encounter probabilities in male *Hypolimnas bolina* (L.) (Nymphalidae). Journal of the Lepidopterists' Society **53**:138-141.

Kruger, F. J., G. J. Breytenbach, I. A. W. Macdonald, and D. M. Richardson. 1989. The characteristics of invaded mediterranean-climate regions. Pages 181-213 in J. A. Drake, and H. A. Mooney, editors. Biological invasions: A global perspective. Wiley, Chichester.

Lach, L. 2007. A mutualism with a native membracid facilitates pollinator displacement by Argentine ants. Ecology **88**:1994-2004.

Lach, L. 2008a. Argentine ants displace floral arthropods in a biodiversity hotspot. Diversity and Distributions **14**:281-290.

Lach, L. 2008b. Floral visitation patterns of two invasive ant species and their effects on other hymenopteran visitors. Ecological Entomology **33**:155-160.

Lach, L., and L. M. Hooper-Bùi. 2010. Consequences of ant invasions. Pages 261-286 in L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant ecology. Oxford University Press, Oxford.

Lach, L., and M. L. Thomas. 2008. Invasive ants in Australia: Documented and potential ecological consequences. Australian Journal of Entomology **47**:275-288.

LeBrun, E. G. 2010. The ecological consequences of cooperative behaviour among workers from different nests. Pages 247-248 in L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant ecology. Oxford University Press, Oxford.

Lee, S. M., and A. Chao. 1994. Estimating population-size via sample coverage for closed capture-recapture models. Biometrics **50**:88-97.

Liang, D., and J. Silverman. 2000. "You are what you eat": Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. Naturwissenschaften **87**:412-416.

Liebherr, J. K., and P. D. Krushelnycky. 2007. Unfortunate encounters? Novel interactions of native *Mecyclothorax*, alien *Trechus obtusus* (Coleoptera : Carabidae), and Argentine ant (*Linepithema humile*, Hymenoptera : Formicidae) across a Hawaiian landscape. Journal of Insect Conservation **11**:61-73.

Longino, J. T. 2000. What to do with the data. Pages 187-203 in D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, D.C.

Majer, J. D. 1994. Spread of Argentine ants (*Linepithema humile*), with special reference to western Australia. Pages 163-173 in D. F. Williams, editor. Exotic ants: Biology, impact, and control of introduced species. Westview Press, Boulder.

Malicky, H. 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden. Tijdschrift Voor Entomologie **112**:213-298.

Menke, S. B., R. N. Fisher, W. Jetz, and D. A. Holway. 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology **88**:3164-3173.

Menke, S. B., and D. A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. Journal of Animal Ecology **75**:368-376.

Migdoll, I. 1992. Field guide to the butterflies of southern Africa. Struik, Cape Town.

Mucina, L., M. L. Rutherford, and L. W. Powrie 2005. Vegetation map of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Oliveras, J., J. M. Bas, and C. Gomez. 2005. Long-term consequences of the alteration of the seed dispersal process of *Euphorbia characias* due to the Argentine ant invasion. Ecography **28**:662-672.

Pedersen, J. S., M. J. B. Krieger, V. Vogel, T. Giraud, and L. Keller. 2006. Native supercolonies of unrelated individuals in the invasive Argentine ant. Evolution **60**:782-791.

Picker, M. D., and M. J. Samways. 1996. Faunal diversity and endemicity of the Cape Peninsula, South Africa - a first assessment. Biodiversity and Conservation **5**:591-606.

Pierce, N. E., M. F. Braby, A. Heath, D. J. Lohman, J. Mathew, D. B. Rand, and M. A. Travassos. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology **47**:733-771.

Pierce, N. E., and W. R. Young. 1986. Lycaenid Butterflies and ants - 2-species stable equilibria in mutualistic, commensal, and parasitic Interactions. American Naturalist **128**:216-227.

Pryke, J. S., and M. J. Samways. 2010. Significant variables for the conservation of mountain invertebrates. Journal of Insect Conservation **14**:247-256.

Roulston, T. H., G. Buczkowski, and J. Silverman. 2003. Nestmate discrimination in ants: Effect of bioassay on aggressive behavior. Insectes Sociaux **50**:151-159.

Roura-Pascual, N., and A. V. Suarez. 2008. The utility of species distribution models to predict the spread of invasive ants (Hymenoptera: Formicidae) and to anticipate changes in their ranges in the face of global climate change. Myrmecological News **11**:67-77.

Roura-Pascual, N., A. V. Suarez, C. Gomez, P. Pons, Y. Touyama, A. L. Wild, and A. T. Peterson. 2004. Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:2527-2534.

Rowles, A. D., and D. J. O'Dowd. 2007. Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. Biological Invasions **9**:73-85.

Rowles, A. D., and D. J. O'Dowd. 2009a. Impacts of the invasive Argentine ant on native ants and other invertebrates in coastal scrub in south-eastern Australia. Austral Ecology **34**:239-248.

Rowles, A. D., and D. J. O'Dowd. 2009b. New mutualism for old: Indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. Oecologia **158**:709-716.

Sanders, N. J., K. E. Barton, and D. M. Gordon. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. Oecologia **127**:123-130.

Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences of the United States of America **100**:2474-2477.

Schilman, P. E., J. R. B. Lighton, and D. A. Holway. 2005. Respiratory and cuticular water loss in insects with continuous gas exchange: Comparison across five ant species. Journal of Insect Physiology **51**:1295-1305.

Seifert, B. 1990. Wie wissenschaftlich wertlose Fangzahlen entstehen - Auswirkungen artspezifischen Verhaltens von Ameisen an Barberfallen direkt beobachtet. Entomologische Nachrichten und Berichte **34**:21-28.

Silverman, J., and R. J. Brightwell. 2008. The Argentine ant: Challenges in managing an invasive unicolonial pest. Annual Review of Entomology **53**:231-252.

Skaife, S. H. 1961. The Argentine ant. Pages 5-13 in S. H. Skaife, editor. The study of ants. Longmans, London.

Skaife, S. H. 1962. The distribution of the Argentine ant *Iridomyrmex humilis* Mayr. Annals of the Cape Provincial Museums **2**:297-298.

Slingsby, P. 1982. The Argentine ant - how much of a threat? Veld & Flora **68**:102-104.

South African National Parks 2010. Table Mountain National Park, Environmental Information System - Fire Management Database as of 2010.

Stanley, M., D. Ward, R. Harris, G. Arnold, R. Toft, and J. Rees. 2008. Optimizing pitfall sampling for the detection of Argentine ants, *Linepithema humile* (Hymenoptera : Formicidae). Sociobiology **51**:461-472.

Steiner, F. M., R. H. Crozier, and B. C. Schlick-Steiner. 2010. Colony structure. Pages 177-193 in L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant ecology. Oxford University Press, Oxford.

Stipinovich, A., and P. Holmes 2009. City of Cape Town's Biodiversity Network. C-PLAN & MARXAN analysis: 2009 Methods & Results. City of Cape Town, Cape Town.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia **85**:74-79.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology **79**:2041-2056.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America **98**:1095-1100.

Suhr, E. L., S. W. McKechnie, and D. J. O'Dowd. 2009. Genetic and behavioural evidence for a city-wide supercolony of the invasive Argentine ant *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) in southeastern Australia. Australian Journal of Entomology **48**:79-83.

Taylor, B. 2010. The ants of (sub-Saharan) Africa (Hymenoptera: Formicidae). Accessed at http://antbase.org/ants/africa/ on 12 October 2010.

Thomas, J. A., and J. C. Wardlaw. 1992. The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. Oecologia **91**:101-109.

Thomas, M. L., and D. A. Holway. 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. Journal of Animal Ecology **74**:532-542.

Touyama, Y., Y. Ihara, and F. Ito. 2008. Argentine ant infestation affects the abundance of the native myrmecophagic jumping spider *Siler cupreus* Simon in Japan. Insectes Sociaux **55**:144-146.

Travassos, M. A., and N. E. Pierce. 2000. Acoustics, context and function of vibrational signalling in a lycaenid butterfly-ant mutualism. Animal Behaviour **60**:13-26.

Trinder-Smith, T. 2006. Wild flowers of the Table Mountain National Park. Botanical Society of South Africa, Cape Town.

Trinder-Smith, T. H. 2003. The Levyns guide to the plant genera of the Southwestern Cape. University of Cape Town, Cape Town.

Tsutsui, N. D., and T. J. Case. 2001. Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. Evolution **55**:976-985.

Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2000. Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences of the United States of America **97**:5948-5953.

van Wilgenburg, E., C. W. Torres, and N. D. Tsutsui. 2010. The global expansion of a single ant supercolony. Evolutionary Applications **3**:136-143.

Vasquez, G. M., and J. Silverman. 2008. Queen acceptance and the complexity of nestmate discrimination in the Argentine ant. Behavioral Ecology and Sociobiology **62**:537-548.

Veile, D. 1991. Ameisen. Grundzüge der Erfassung und Bewertung. Pages 177-188 in J. Trautner, editor. Arten- und Biotopenschutz in der Planung: Methodische Standards zur Erfassung von Tierartengruppen. Margraf, Weikersheim.

Vogel, V., J. S. Pedersen, P. d'Ettorre, L. Lehmann, and L. Keller. 2009. Dynamics and genetic structure of Argentine ant supercolonies in their native range. Evolution **63**:1627-1639.

Wagner, D., and L. Kurina. 1997. The influence of ants and water availability on oviposition behaviour and survivorship of a facultatively ant-tended herbivore. Ecological Entomology **22**:352-360.

Walters, A. C. 2006. Invasion of Argentine ants (Hymenoptera : Formicidae) in South Australia: Impacts on community composition and abundance of invertebrates in urban parklands. Austral Ecology **31**:567-576.

Walters, A. C., and D. A. Mackay. 2003a. An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): Comparisons with a native *Iridomyrmex* species in South Australia. Insectes Sociaux **50**:355-360.

Walters, A. C., and D. A. Mackay. 2003b. The impact of the Argentine ant, *Linepithema humile* (Mayr), on native ants and other invertebrates in South Australia. Records of the South Australian Museum Monograph Series **7**:17-24.

Walters, A. C., and D. A. Mackay. 2004. Comparisons of upper thermal tolerances between the invasive Argentine ant (Hymenoptera : Formicidae) and two native Australian ant species. Annals of the Entomological Society of America **97**:971-975.

Walters, A. C., and D. A. Mackay. 2005. Importance of large colony size for successful invasion by Argentine ants (Hymenoptera : Formicidae): Evidence for biotic resistance by native ants. Austral Ecology **30**:395-406.

Ward, D. F., and R. J. Harris. 2005. Invasibility of native habitats by Argentine ants, *Linepithema humile*, in New Zealand. New Zealand Journal of Ecology **29**:215-219.

Ward, P. S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia **55**:1-16.

Williams, M. C., and J. G. Joannou. 1996. Observations on the oviposition behaviour and larvae of *Thestor basutus capeneri* Dickson (Lepidoptera: Lycaenidae: Miletinae) in South Africa. Metamorphosis **7**:12-16.

Wynhoff, I., M. Grutters, and F. van Langevelde. 2008. Looking for the ants: Selection of oviposition sites by two myrmecophilous butterfly species. Animal Biology **58**:371-388.

Yahner, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology **2**:333-339.

Zee, J., and D. Holway. 2006. Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*. Insectes Sociaux **53**:161-167.

Appendix 1. Lycaenidae occurring on the Cape Peninsula

Species	Distribution[1]	Ant Association[2]	Associated Ant[2]	Flight Period (Months)	Conservation Status
Aloeides almeida[3]	Table Mountain Range[C]	-	-	late IX-IV[C]	-
A. aranda[3]	Twelve Apostles[C]	obligate[D]	*Pheidole capensis*[C]	late IX - IV[C]	-
A. egerides	not recorded from study area	-	-	X-IV[C]	Vulnerable[H], Rare[J], endemic (Western Cape)[J], Protected[J]
A. pierus[3]	Table Mountain Range[A]	obligate[D]	*Lepisiota capensis*[C]	late IX - IV[C]	-
A. thyra thyra[3]	Table Mountain Range[A]	obligate[D]	*Lepisiota capensis*[A]	late VIII - V[C]	-
Anthene definita definita[4]	Cape Peninsula[C]	facultative[D]	*Camponotus maculatus*[C]	I - XII[A]	-
			Lepisiota capensis[C]		
			Pheidole capensis[C]		
			Linepithema humile[A]		
Cacyreus dicksoni	Twelve Apostles[A]	-	-	I-XII[C]	-
C. lingeus	Cape Peninsula[C]	-	-	I-XII[C]	-
C. marshalli	Table Mountain Range[A]	-	-	I-XII[A]	-
C. palemon palemon	Table Mountain Range[A]	-	-	VIII-V[C]	-
Capys alphaeus	Western Cape[C]	-	-	I-XII[A]	-
Chrysoritis chrysaor	not recorded from study area	obligate[D]	*Crematogaster liengmei*[D]	spring and summer[C]	-
C. felthami felthami	not recorded from study area	obligate[D]	*Crematogaster peringueyi*[D]	late IX-IV[C]	-
C. nigricans nigricans	not recorded from study area	obligate[D]	*Crematogaster* sp.[A]	IX-IV[A]	Indeterminate[J], endemic (Cape Peninsula)[J], Protected[J]
C. palmus palmus[3]	not recorded from study area	obligate[D]	*Crematogaster peringueyi*[A]	IX - IV[C]	-
			Crematogaster liengmei[D]		
C. pyroeis pyroeis	not recorded from study area	obligate[D]	*Myrmicaria nigra*[D]	IX-IV[C]	-
C. thysbe thysbe	not recorded from study area	obligate[D]	*Crematogaster peringueyi*[D]	VIII-V[C]	-
C. zeuxo[4]	Table Mountain Range[A]	obligate[D]	*Crematogaster liengmei*[D]	late IX - I[C]	Endangered[J]
			Crematogaster spp.[C]		
C. zonarius	not recorded from study area	obligate[D]	*Crematogaster peringueyi*[D]	IX-XI[C]	endemic (Western Cape)[C]
Eicochrysops messapus messapus	Table Mountain Range[A]	-	-	IX-V[C]	-
Lampides boeticus[4]	Table Mountain Range[A]	facultative[D]	*Lepisiota capensis*[C]	I - XII[A]	-
			Linepithema humile (?)[F]		
Lepidochrysops methymna methymna[4]	Table Mountain Range[A]	obligate[D]	*Camponotus maculatus*[G]	late IX - I[C]	-
L. oreas oreas[4]	Table Mountain Range[A]	obligate[C]	*Camponotus maculatus*[D]	X - I[C]	-
			Camponotus niveosetosus[A]		
L. robertsoni[4]	Table Mountain Range[A]	obligate[C]	*Camponotus niveosetosus*[C]	X - I[C]	-
L. trimeni[4]	Twelve Apostles[B]	obligate[D]	*Camponotus maculatus*[G]	IX - II[A]	-
			Camponotus niveosetosus[F]		
Leptomyrina lara	Cape Peninsula[C]	-	-	I-XII[A]	-
Leptotes brevidentatus	Cape Peninsula[C]	-	-	?	-
L. pirithous	Cape Peninsula[C]	-	-	I-XII[C]	-
Lycaena orus	Table Mountain Range[C]	-	-	I-XII[C]	-
Phasis thero thero	not recorded from study area		*Crematogaster* spp.[C]	VIII-IV[C]	-
Tarucus thespis[3]	Cape Peninsula Mountains[C]	facultative[D]	*Linepithema humile* (1 record)[E]	I - XII[C]	-
Thestor protumnus protumnus	not recorded from study area		*Anoplolepis custodiens*[C]	IX-XII[C]	-
T. yildizae	Twelve Apostles[A]	obligate[D]	*Anoplolepis custodiens*[A]	late XI - II[A]	Vulnerable[H], Rare[J], endemic (Cape Peninsula) Vulnerable[J], endemic (Cape Peninsula)[J], Protected[J]
Trimenia malagrida malagrida	not recorded from study area	obligate[D]	*Anoplolepis custodiens*[C]	II-IV[C]	-
Zizeeria knysna	Cape Peninsula[C]	-	-	I-XII[C]	-

[1] Only locations including study site are given

[2] Only associations with documented ant species are given

[3] Myrmecophilous species observed in study area

[4] Myrmecophilous species not oberved in study area, although sampling period within flight period of butterfly and species recorded from study site

References: [A] (Claassens & Dickson 1980), [B] (Claassens 1976), [C] (Claassens 2000), [D] (Heath & Claassens 2003), [E] (Dickson 1944), [F] (Clark & Dickson 1971), [G] (Claassens & Dickson 1974), [H] (IUCN 2010), [J] (Henning & Henning 1989)

Appendix 2. Ant species observed and their abundance within transects.

Species	Transect									
	1	2	3	4	5	6	7	8	9	10
Subfamily Dolichoderinae										
Linepithema humile	17	1	-	78	-	3	-	-	-	-
Technomyrmex pallipes	1	-	-	-	-	-	-	12	-	-
Subfamily Formicinae										
Camponotus bertolonii	-	-	-	-	-	-	-	-	-	1
C. maculatus group sp. 1	-	-	3	-	2	2	-	-	-	2
C. maculatus group sp. 2	5	-	-	-	5	-	-	-	-	-
C. maculatus group sp. 3	-	-	1	-	-	6	-	-	4	2
C. maculatus group sp. 4	-	-	-	1	1	-	1	-	2	1
C. niveosetosus	2	-	-	8	12	-	-	1	1	1
C. rufoglaucus group sp. 1	-	3	-	16	9	1	-	-	-	-
Lepisiota capensis	28	-	51	8	143	213	123	4	45	17
Lepisiota sp. 1	-	176	-	4	1	1	-	-	-	-
Plagiolepis sp. 1 (nr *deweti*)	-	-	-	-	-	6	-	-	1	2
Subfamily Myrmicinae										
Meranoplus peringueyi	15	12	5	13	21	1	-	-	-	2
Messor capensis	-	-	-	-	2	-	-	-	-	-
Monomorium boerorum	-	13	-	-	-	-	-	-	-	-
M. excensurae	-	-	-	-	-	3	-	-	-	-
M. fastidium	9	1	-	-	-	-	3	4	1	-
M. paternum	-	-	-	-	-	-	1	-	-	1
M. rhopalocerum	-	2	-	-	-	-	-	-	4	6
Monomorium sp. 1	-	-	-	8	2	-	-	-	-	-
M. tablense	7	-	2	-	-	-	-	-	-	-
Ocymyrmex barbiger	3	15	-	47	38	25	3	-	9	-
Pheidole capensis	4	63	81	87	3	123	157	-	1	-
P. megacephala	39	89	-	-	158	-	-	34	180	57
Pheidole. sp. 1	-	1	-	-	-	-	-	-	-	-
Rhoptromyrmex sp. 1	-	-	-	-	-	-	-	94	-	82
Solenopsis punctaticeps	33	1	1	-	-	2	2	-	-	1
Tetramorium capense	5	6	3	1	9	2	-	12	5	10
T. erectum	-	-	-	1	-	-	-	1	-	-
T. regulare	-	13	3	13	1	1	-	1	-	4
T. sericeiventre	24	30	1	102	15	-	-	5	3	3
T. simillimum group sp. 1	-	-	-	11	-	-	-	-	-	-
Subfamily Ponerinae										
Hypoponera sp. 1	-	-	-	-	1	-	-	-	-	1
Pachycondyla pumicosa	-	-	-	-	-	-	-	5	-	-
Total	192	426	151	398	423	389	290	173	256	193